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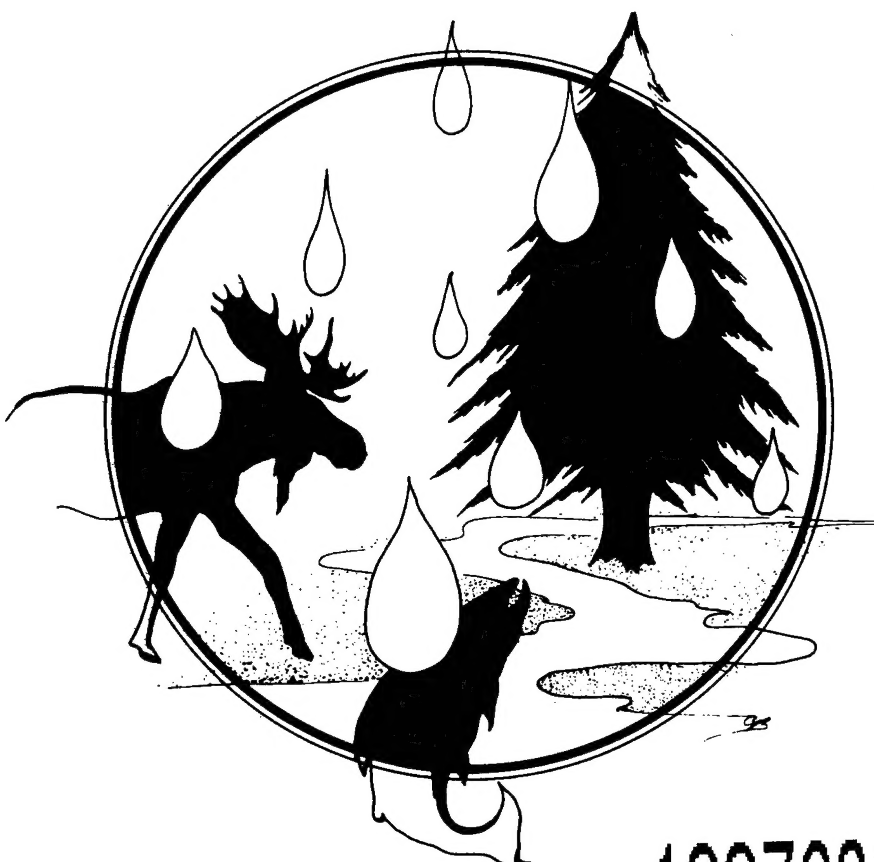
Thermal Stratification of Dilute Lakes—Evaluation of Regulatory Processes and Biological Effects Before and After Base Addition: Effects on Brook Trout Habitat and Growth



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Air Pollution and Acid Rain
Report 29

Thermal Stratification of Dilute Lakes—Evaluation of Regulatory Processes and Biological Effects Before and After Base Addition: Effects on Brook Trout Habitat and Growth

By

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Thermal Stratification of Dilute Lakes—Evaluation of Regulatory Processes and Biological Effects Before and After Base Addition: Effects on Brook Trout Habitat and Growth

by

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Abstract. We address the significance of changes in summer thermal stratification patterns of Adirondack lakes affected by acidification to cold-water fish populations inhabiting these sensitive lakes. The brook trout (*Salvelinus fontinalis*) is the primary cold-water fish species indigenous to acid-sensitive lakes in the Adirondack region of northern New York State; the ability of these lakes to sustain this important sport species is highly dependent on the availability of adequate summer habitat, consisting of cool, well-oxygenated water.

We hypothesized that acidification-induced reductions in the thermal stability of sensitive Adirondack lakes could lead to degradation of potential brook trout habitat. We also hypothesized, on the basis of energetic considerations, that brook trout growth and average size at age would be sensitive indicators of differences in the extent and availability of preferred summer habitat in lakes with different thermal structures.

These hypotheses were addressed in this study by utilizing data available from previous lake liming studies in the Adirondack region, brook trout growth data from management studies in the region, and the extensive Adirondack Lake Survey Corporation (ALSC) data base. We compared brook trout growth among lakes with known thermal stratification patterns; analyzed temporal changes in the extent and availability of preferred brook trout habitat, resulting from changes in acid or base status of limed Adirondack lakes; and applied a bioenergetic growth model for sensitivity analysis of temperature effects on simulated growth of brook trout populations inhabiting lakes with different thermal structures.

Analyses of the relation between stratification status of ALSC lakes and water color indicated that shallow, low-color lakes were most sensitive to changes in thermal stratification status induced by acidification-related changes in water color and transparency. This finding was confirmed by observations of changes in color, transparency, and thermal stratification in limed lakes after neutralization and reacidification, where significant changes in transparency and thermal stratification status were observed only in low-color lakes.

More than 70% of the small, shallow ALSC lakes were classified as predominantly weakly stratified systems that would be potentially sensitive to changes in thermal stratification status resulting from relatively small changes in color and transparency. On the basis of historical trends of decreased water color in one Adirondack drainage system, it was estimated that if comparable changes in color had occurred in these sensitive lakes, about 22% more strongly stratified lakes would have been present in the 1940's than are now present in the region.

Preferred thermal habitat for brook trout was defined as the lake region within the temperature range of 10–16° C, having dissolved oxygen levels greater than 5 ppm. Experimental liming studies demonstrated that the temporal availability and volumetric extent of this habitat is significantly increased as a result of decreased transparency and increased thermal stability after liming of shallow, low-color lakes. Reacidification of these lakes resulted in decreases in the availability of preferred brook trout habitat. Comparisons of brook trout growth in unstratified and stratified Adirondack lakes revealed significantly greater mean weights for older (> age 2), larger brook trout in stratified lakes, but no significant effects of stratification on growth of younger (age 1) trout. The smaller fish did not seem to be constrained by the observed range of midsummer thermal conditions in Adirondack lakes, but growth seemed to be strongly density-dependent.

Simulations of brook trout growth in unstratified and stratified lakes also predicted an increasing differential in weight at age between the lake stratification types as a result of summer reductions in growth rate of brook trout in warm, unstratified lakes. This analysis also suggested that sustained growth in unproductive Adirondack waters of older brook trout (> age 2), beyond an approximate threshold of 500–600 g body weight, requires the availability of low (<16° C) summer water temperatures that would be available only in stratified lakes.

Both high population density and limitations in the temporal availability or spatial extent of preferred thermal habitat in shallow Adirondack lakes are of primary significance in determining population growth patterns and limiting maximum size at age for older age classes of brook trout. Brook trout populations presently most susceptible to negative effects from acidification-induced increases in transparency and consequent reductions in preferred thermal habitat occur primarily in shallow, low-color lakes that are marginally acidified and either weakly stratified or strongly stratified with anoxic hypolimnia. As judged from results of experimental liming studies, significant improvements in brook trout thermal habitat could be achieved in these lakes by reducing acidity levels.

Key words: Acidification, Adirondack region, brook trout, lakes, liming, thermal stratification.

Several studies have documented that increased transparency often accompanies the acidification of lakes (Schofield 1972; Almer et al. 1974; Malley et al. 1982; Yan 1983; Shearer et al. 1987) and experimental liming studies have demonstrated the reversibility of this relation (Schofield et al. 1989; Driscoll et al. 1990). These acid–base-related shifts in transparency are believed to occur as a result of changes in water color due to increases or decreases in dissolved organic carbon and phytoplankton production (Bukaveckus and Driscoll 1990). Changes in transparency may also alter the thermal characteristics of lakes affected by acidification; concern for the effects that thermal structure changes might have on cold-water fish species endemic to waters affected by acidification has been expressed (Effler and Owens 1985; Bukaveckus and Driscoll 1990; Driscoll et al. 1990). Modeling studies completed during the first phase of this study (Driscoll et al. 1990) indicated that modest changes in light attenuation of shallow (5–10 m maximum depth) Adirondack lakes could cause significant changes in summer thermal stratification patterns. This prediction was supported by observed decreases in transparency and shifts from weak or unstratified conditions to strong thermal stratification after liming of previously acidic lakes. Reacidification of these limed lakes resulted in a return to unstratified or weak thermal stratification patterns, associated with increased transparency.

Species existing at the geographic limits of their natural distribution tend to be particularly vulnerable to changes in limiting environmental factors (MacCrimmon et al. 1971). The southern extent of lake-dwelling populations of brook trout (*Salvelinus fontinalis*) is limited by temperature to northern New York State, and their distribution further southward is limited primarily to headwater streams (MacCrimmon and Campbell 1969;

Power 1980). The brook trout is the primary coldwater sport fish indigenous to small, shallow Adirondack lakes; the ability of these lakes to sustain viable brook trout populations is highly dependent on the availability of summer habitat with cool, well-oxygenated water.

Because fish are poikilotherms, the amount of energy required to maintain basal metabolism is determined by the temperature of their environment. With an increase in temperature more energy is required for basic metabolic processes and less energy is available for growth. In summer, fish move into thermal habitats that best suit their metabolic requirements (Magnuson et al. 1979; Coutant and Benson 1990). For species whose metabolic optimal temperature occurs within or below the metalimnion, population size and individual growth rates may be determined by habitat limitations in late summer when the volume of cold water available is at a minimum. The crowding of fish into limited summer thermal refugia can also contribute to increased disease, intraspecific competition, deteriorating body condition as food sources are exhausted, overfishing, increased catch and release mortality, and even decreased survival of eggs and larvae presumably due to energetic deficits of females during egg development (Magnuson et al. 1979; Coutant and Benson 1990).

On the basis of laboratory growth studies and field observations of summer distribution, the preferred temperature range for brook trout is about 10–16° C, at dissolved oxygen levels greater than 5 ppm (MacCrimmon and Campbell 1969; Cherry et al. 1977; Coutant 1977; Cone 1987). These preferred environmental conditions are generally found within the metalimnetic region of stratified Adirondack lakes during summer months. Conversely, minimum water column temperatures in unstratified Adirondack lakes generally exceed the preferred temperature range for brook trout in late summer. Although brook trout can survive at these higher temperatures, below the lethal limit, increased energy costs for basal metabolism would probably result in less energy for growth. This limitation would be most severe for older, larger fish that metabolize less efficiently at higher temperatures than smaller fish (Baldwin 1956). Given these observations, we hypothesized that brook trout growth and average size at age should be sensitive indicators of differences in the extent and availability of preferred summer thermal habitat in stratified and unstratified Adirondack lakes.

The presence or absence of brook trout in an ecosystem is commonly used to indicate the quality of the environment. Environmental conditions that may limit the growth, survival, and distribution of brook trout, but do not result in their extinction from a body of water, can be overlooked. An ancillary effect of acidification that has not been previously investigated is the degradation of brook trout thermal habitat. The relevance and potential severity of this phenomenon in the Adirondack region were explored in this study. Specifically, we analyzed the effects of acid–base-related changes in the thermal structure of Adirondack lakes on the availability of summer habitat for brook trout and the resulting growth characteristics of populations inhabiting these lakes.

Methods

Description of Study Lakes

Four groups of lakes were selected for study: all Adirondack Lake Survey Corporation (ALSC) lakes with brook trout present (N = 577), the Adirondack Fishery Research Program (AFRP) lakes managed intensively for brook trout (N = 11), the Extensive Liming Study (ELS) lakes stocked with brook trout (N = 9), and the Lake Acidification Mitigation Project (LAMP) lakes managed for brook trout (N = 2). General morphometric features, brook trout population status, and base addition histories for the AFRP, ELS, and LAMP lakes are provided in Table 1; characteristics of the ALSC lakes were summarized by Gallagher and Baker (1990).

The AFRP lakes, managed intensively for brook trout, are on private lands in the southwestern Adirondack Mountain region. Most of the lakes lack natural reproduction but have had a sustained presence of brook trout for 10 to 35 years through maintenance stocking of fall fingerlings (N = 8). Some of the lakes have brook trout populations supported entirely (N = 1) or partially (N = 2) by natural reproduction. Those lakes threatened by acidification have been limed, either on an annual basis since the early 1970's (N = 3) or sporadically since the late 1950's (N = 6) to maintain adequate water quality for brook trout survival. Some lakes are marginally acidic yet have not been limed; these serve as "acid controls" (N = 2). The AFRP lakes range from 2.6 to 133.2 ha with maximum depths of 5.0 to 13.5 m.

Table 1. *Morphometry, brook trout population status, and base addition history for lakes of the Adirondack Fishery Research Program, (AFRP), the Extensive Liming Study (ELS), and the Lake Acidification Mitigation Project (LAMP).*.

Lake group	S.A. (hectares)	Depth (meters) Mean	Depth (meters) Maximum	Brook trout population status	Base addition history (tons)
AFRP lakes					
Canachagala	133.2	4.3	13.5	Stocked (80%) Natural (20%)	Occasional (10–40)
Chambers	10.4	3.6	9.0	Stocked (45%) Natural (55%)	Occasional (5–10)
Deer	13.2	3.6	5.0	Stocked (100%)	Annual (5–8)
Fourth Bisby	24.3	2.9	8.25	Stocked (100%)	Annual (5–8)
Goose	6.1	—	5.0	Stocked (100%)	Unlimed (0)
Green	10.3	5.5	12.5	Stocked (100%)	Occasional (2–10)
Jones	22.9	1.9	9.0	Natural (100%)	Occasional (10–21)
Mountain	3.4	—	7.0	Stocked (100%)	Annual (5–8)
Otter	9.6	3.5	10.4	Stocked (100%)	Unlimed (0)
Rock	76.9	2.0	5.2	Stocked (100%)	Occasional (10–20)
Wheeler	2.6	—	5.2	Stocked (100%)	Occasional (6)
ELS lakes					
Big Chief	1.2	4.4	11.0	Stocked (100%)	Fall 1983 (4.54)
Mountain	6.0	4.7	8.5	Stocked (100%)	Fall 1983 (12.02)
Highrock	4.0	3.5	8.2	Stocked (100%)	Fall 1983 (7.26)
Trout	3.7	1.3	5.0	Stocked (100%)	Fall 1983 (4.99)
Silver Dollar	0.5	4.1	8.5	Stocked (100%)	Fall 1984 (2.72)
Pocket	1.2	2.9	11.6	Stocked (100%)	Fall 1984 (6.35)
Jones	5.3	6.4	14.7	Stocked (100%)	Fall 1984 (17.69)
Indigo	5.7	3.7	6.0	Stocked (100%)	Fall 1984 (9.30)
Barto	5.5	2.9	6.5	Stocked (100%)	Fall 1984 (13.11)
LAMP lakes					
Woods	23.0	2.3	11.6	Stocked (100%)	Spring 1985 (23.0)
Cranberry	10.0	2.9	7.6	Stocked (100%)	Spring 1985 (7.0)

The ELS lakes are in the same geographic region as the AFRP lakes. These lakes were all acidified, fishless waters before lime applications and annual fall fingerling brook trout plants, beginning in 1983 ($N = 4$) and 1984 ($N = 5$). The lakes received one application of lime and were allowed to reacidify to evaluate the rate of reacidification and effects on the stocked brook trout populations. The ELS lakes range from 0.5 to 6.0 ha with maximum depths of 5.0 to 14.7 m. Schofield et al. (1986) and Gloss et al. (1989a) provide detailed results of the Extensive Liming Study.

The two LAMP lakes (Woods Lake and Cranberry Pond) were acidic, fishless waters before initial liming and stocking with brook trout in spring 1985. Cranberry Pond received only one treatment (as in the ELS lakes) and reacidified in fall 1985. Woods Lake received maintenance liming treatments and annual stocking through 1990. Descriptions of these waters and the treatment responses are presented in Driscoll et al. (1989) and Gloss et al. (1989b).

Water Quality Measurements

Water quality surveys were conducted on ALSC, AFRP, ELS, and LAMP lakes during open-water periods. Temperature (° C) profiles were measured at 0.5 m intervals in the ALSC and AFRP lakes in July or August, when water temperatures were most limiting for brook trout. More frequent temperature profiles were meas-

ured throughout the open-water period in ELS and LAMP lakes. Additional parameters measured were Secchi depth (meters), apparent color, and pH and dissolved oxygen (ppm) at the surface, thermocline, and bottom. Water quality surveys were routinely conducted for ELS (monthly) and LAMP (3-week intervals) lakes. Water samples were analyzed for dissolved oxygen, pH, and other parameters (ELS, Schofield et al. 1986; LAMP, Driscoll et al. 1989).

Classification of Lakes Based on Thermal Stratification

Both observed summer thermal profiles and Secchi depth measurements were used to determine thermal stratification classes for ALSC, AFRP, ELS, and LAMP lakes, by using EPA Eastern Lakes Survey stratification criteria (Linthurst et al. 1986) and the UFILS1 thermal stratification model (Driscoll et al. 1990). The three thermal stratification categories were defined as follows:

Strongly stratified: temperature difference between 1.5 m and 60% of maximum depth greater than or equal to 4° C;

Weakly stratified: temperature difference between 1.5 m and 60% of maximum depth less than 4° C and difference between 1.5 m and maximum depth greater than or equal to 4° C;

Unstratified: temperature difference between 1.5 m and maximum depth less than 4° C.

Predicted boundaries for these stratification classes, as a function of lake maximum depth and Kd (Kd estimated from the regression function log(Kd) = 0.140–0.081 log (Secchi depth, meters), were determined by Driscoll et al. (1990) using the UFILS1 thermal stratification model. Observed changes in transparency and thermal classification, before and after base additions, were determined for selected AFRP, ELS, and LAMP lakes.

A multinomial logistic regression model (Steinberg 1988) of stratification class as a function of true water color and maximum depth was developed from the ALSC summer lake survey data to evaluate the effects of historical and liming-induced acid–base-related changes in water color on thermal stratification patterns. The multinomial logistic model was designed for subjective categorical response variables (thermal stratification class in this instance) and provided a means of estimating the predicted probabilities that a lake would fall into a given stratification class, based on estimates of maximum depth and water color. Numerical indices assigned to each stratification class were 1 = strongly stratified, 2 = weakly stratified, and 3 = unstratified. The coefficient estimates (Table 2) produced by the multinomial logistic regression model differ considerably from linear regression models in that a complete set of coefficients is estimated for each choice class but one. The left out, or reference, option is indexed by the greatest permissible value of the dependent variable (3 in this instance). The null hypothesis that all model coefficients except the constant are equal to zero was evaluated by a log likelihood ratio chi-square test. Frequency distributions for ALSC lakes by predicted thermal stratification class were generated by simply summing the predicted probabilities for each stratification class.

Determinations of Volume and Area of Preferred Thermal Habitat for Brook Trout

The volume of summer habitat relative to the total lake volume is often used when determining the carrying capacity of brook trout lakes. Relative levels of natural recruitment, competition, and lake fertility are considered along with relative summer habitat volume when calculating stocking rates for brook trout lakes in New York State (Keller 1979). The volume of summer brook trout habitat in Adirondack waters is usually determined by temperature constraints.

Coutant (1977) compiled temperature preference data from the available literature for a number of fish species. The final preferendum for adult brook trout in two natural environments was determined to be 14–16° C (Ferguson 1958; Spigarelli 1975, as cited by Coutant 1977). In vertical gill-netting studies on an Adirondack lake, Cone (1987) observed that brook trout were concentrated within the metalimnion at 10–15° C. He also noted that brook trout were essentially absent from waters with dissolved oxygen levels less than 5 ppm. Baldwin (1956) observed maximum growth of brook trout at 13° C. On the basis of these studies, we considered the preferred temperature range for brook trout to be about 10–16° C, where dissolved oxygen levels are above 5 ppm.

The 10 and 16° C isopleths, obtained from thermal profile information, defined the boundaries of preferred brook trout thermal habitat. To visualize seasonal and annual fluctuations in depth as well as depth range of preferred habitat, preferred habitat isopleths were produced for ELS and LAMP

Table 2. *Multinomial logistic model of stratification class (unstratified, weakly stratified, strongly stratified) as a function of true color and maximum depth for Adirondack Lake Survey Corporation lakes. Stratification class is assigned on the basis of Kd per maximum depth boundaries for strongly stratified and unstratified lakes, as defined by Driscoll et al. (1990).*

Summary of Fit				
Rsquare (U) .7952626				
Observations 1033				
Analysis of LogLikelihood				
Source	DF	-LogLikelihood	ChiSquare	Prob>ChiSq
Model	4	850.2539	1,700.507	0.000000
Error	1027	218.8947		
C Total	1031	1,069.1486		
Parameter Estimates				
Term	Estimate	Std Error	ChiSquare	Prob>ChiSq
Intercept	-34.373464	3.7259998	85.11	0.0000
log(1+x) of Color	4.24793750	0.62153536	46.71	0.0000
log(x) of Max D	30.1956004	3.2130314	88.32	0.0000
Intercept	25.9814282	2.6607106	95.35	0.0000
log(1+x) of Color	-4.2102291	0.58297819	52.16	0.0000
log(x) of Max D	-29.614119	2.8856658	105.32	0.0000
Effect Test				
Source	Nparm	DF	Wald ChiSquare	Prob>ChiSq
log(1+x) of color	2	2	98.59145	0.0000
log(x) of Max D	2	2	192.15439	0.0000

lakes. Hypsographic curves (depth–area, depth–percent area, depth–volume, depth–percent volume) were developed, as described by Wetzel and Likens (1979), from detailed bathymetric data for ELS (Schofield et al. 1986), LAMP (Staubitz and Zarriello 1989), and AFRP (field station archives) lakes. Seasonal and annual fluctuations in the size of preferred brook trout habitat were derived from these curves for ELS and LAMP waters. Percent area and percent volume of the preferred habitat relative to total lake area and volume were used when making cross-lake comparisons.

Brook Trout Population Evaluation

Fall and spring trapnet inventories were conducted to measure length (millimeters), weight (grams), and other vital population statistics for brook trout in the AFRP, ELS, and LAMP lakes. Sampling procedures were previously described for AFRP (Flick and Webster 1976), ELS (Schofield et al. 1986; Gloss et al. 1989b), LAMP (Schofield et al. 1989), and ALSC (Baker et al. 1990) lakes. Pooled samples were used to calculate mean length and weight at age of brook trout for strongly stratified, weakly stratified, and unstratified lakes.

Comparisons of Brook Trout Mean Weight at Age

Comparisons of log transformed mean weight at age for fall captured brook trout, by stratification class, were made for AFRP and ELS lakes using one way ANOVA (Snedecor and Cochran 1980). Brook trout were sampled in the ALSC lakes from April to November, so a factorial ANOVA with capture date (Season) and stratification class as dependent variables was employed for comparisons of mean weight at age. The effects of presence or absence of natural reproduction in these lakes was also evaluated as a third dependent variable potentially affecting growth, since lakes with naturally reproducing brook trout populations tend to have higher population density than lakes maintained by stocking (Schofield 1990).

Effects of Preferred Thermal Habitat Availability and Stocking Density on Brook Trout Mean Weight at Age

The relations between age-specific brook trout growth, the minimum volume of preferred thermal habitat during the summer, and stocking density

in the AFRP lakes were determined by regression analysis. Lakes were excluded from the analysis if natural reproduction exceeded 20%; Chambers and Jones lakes were not included in this regression analysis. The variables in the analyses were defined as follows:

Dependent variable
$Y1$ = mean weight for $fall_n$ (gm) [log transformed]
Independent variables
$X1$ = volume of preferred thermal habitat for $summer_n$ (m^3)
$X2$ = percent volume of preferred thermal habitat for $summer_n$ (m^3)
$X3$ = stocking density for $fall_{n-1}$ (pounds/ha)
$X4$ = age-specific cumulative stocking density (pounds/ha) as shown below:
$X4$ for age 1+ = pounds stocked $fall_{n-1}$
$X4$ for age 2+ = pounds stocked $fall_{n-1}$ + pounds stocked $fall_{n-2}$
$X4$ for age 3+ = pounds stocked $fall_{n-1}$ + pounds stocked $fall_{n-2}$
pounds stocked $fall_{n-3}$
$X4$ for age 4+ = pounds stocked $fall_{n-1}$ + pounds stocked $fall_{n-2}$
pounds stocked $fall_{n-3}$ + pounds stocked $fall_{n-4}$

The dependent variable ($Y1$) was the mean weight at age in the $fall_n$ trapnet sample. The observed mean weights were log transformed to account for skewed distributions. The observed weights in a sample reflect the influence of thermal conditions that existed during the previous $summer_n$. Independent variable $X1$ represents the observed volume of preferred thermal habitat, whereas $X2$ represents the percent volume of preferred thermal habitat (i.e., relative to total lake volume). The observed weight in the $fall_n$ sample was also influenced by the stocking density in previous years. Independent variable $X3$ represents the stocking density for the $fall_{n-1}$ immediately preceding the $fall_n$ trapnet sample. Independent variable $X4$ represents the cumulative stocking density for specific-age fish in fall $seasons_{n-x}$ preceding the $fall_n$ trapnet sample. The assumption was made that fall fingerlings would exert the greatest predation effect on the forage base of a lake for the first year after stocking. Thus, cumulative stocking density ($X4$) and its relation to observed mean weight ($Y1$) for age 1+ fish would be based on the density of those fish stocked the previous fall (i.e., $fall_{n-1}$). Further, for age 4+ fish the relation between cumulative stocking density ($X4$) and observed mean weight ($Y1$) would be the cumulative effect of stocking successive year classes of fall fingerling brook trout from the time the age 4+ group was first stocked (i.e., $fall_{n-1}$ + $fall_{n-2}$ + $fall_{n-3}$ + $fall_{n-4}$).

Regression Analysis

Simple, multiple, and stepwise regression analysis screening techniques (Snedecor and Cochran 1980) were used to determine the relation between mean weight ($Y1$) and the volume of preferred thermal habitat ($X1$), the percent volume of preferred habitat ($X2$), the stocking density ($X3$), and the cumulative stocking density ($X4$) in AFRP lakes for age 1+, 2+, 3+, and 4+ fish. These three techniques provided an evaluation of the correlation and degree of variation in growth accounted for by each variable. The regression statistics were used only as screening tools to detect significant relation, not to develop predictive equations.

Model Sensitivity Analyses of Thermal Habitat Availability Effects on Brook Trout Growth

A bioenergetic growth model developed by Kerr (1971) and calibrated for brook trout growth analysis (Schofield et al. 1989) was employed to evaluate the effects of thermal habitat availability in Adirondack lakes on brook trout growth and weight at age. Model parameters and coefficients used in these analyses are as given by Schofield et al. (1989). All model simulations were conducted using the Stella II model development and simulation software package (High Performance Systems, Inc. 1990) for the Macintosh computer. The primary variables affecting growth in this model are temperature, fish size, prey size, and prey density. Two model configurations were used to estimate maintenance temperatures as a function of fish weight for ranges of prey sizes and densities representative of Adirondack brook trout lakes, and to simulate brook trout growth and preferred temperatures in strongly stratified, weakly stratified, and unstratified lakes with equal prey resources. Maintenance temperature was defined as the temperature where growth is zero for fish of a given body weight feeding on specified prey of constant size and density. Preferred temperature was defined as the temperature where growth rate was maximum for fish of a given size and constant prey resource. In the model simulations, brook trout "selected" the preferred temperature within monthly minimum and maximum water column temperature boundaries defined for lakes of differ-

ent stratification classes. These seasonal temperature cycles were repeated over a 4-year simulation period for each lake. All model simulations were initiated with yearling fish weighing 100 g, and preferred temperature and growth estimates were calculated on a daily basis.

Results

Classification of Lakes Based on Thermal Stratification

Light attenuation coefficients (Kd) were calculated for all ALSC lakes having summer Secchi depth measurements ($N = 1{,}034$) and then classified as strongly stratified, weakly stratified, or unstratified based on the UFILS1 model Kd and maximum depth boundaries. This data set was then used to generate the logistic model of lake stratification class as a function of summer water color and maximum depth. Summing the predicted probabilities from the logistic model by stratification class yielded a frequency distribution of lakes identical to the calibration data set. Because all ALSC lakes ($N = 1{,}468$) had summer measurements of water color, but not Secchi disk transparency, the logistic model was used to calculate stratification class probability values for each lake, a lake was then assigned to the stratification class having the highest predicted probability greater than or equal to 0.5. Comparison of the predicted stratification class distributions for all ALSC lakes and only those ALSC lakes containing brook trout ($N = 577$) indicates that both groups have a high (>40%) proportion of unstratified lakes, but there are proportionally more stratified waters in the brook trout lakes (Table 3). Median maximum depths for ALSC brook trout lakes classified as unstratified, weakly stratified, and strongly stratified were: 2.1, 6.3, and 14.1 m (Fig. 1); median minimum summer water column temperatures for the same respective classes were 20.0, 12.8, and 7.0° C (Fig. 2). Most of the shallow, unstratified lakes do not have summer habitat within the preferred (10–16° C) temperature range for brook trout.

Water quality surveys provided sufficient information to classify the AFRP and ELS lakes by using both the EPA temperature criteria and the UFILS1 model boundaries based on Kd and maximum depth. The thermal classifications of the AFRP and ELS lakes are presented in Tables 4 and 5. There was general agreement in the thermal classification of AFRP lakes using the UFILS1 model and EPA temperature criteria.

Table 3. *Stratification class distributions for all Adirondack Lake Survey Corporation (ALSC) lakes and ALSC lakes containing brook trout. Stratification classes are based on UFILS1 model Kd–maximum depth boundaries.*

	All ALSC lakes		ALSC brook trout lakes	
Stratification class	*N*	(%)	*N*	(%)
Unstratified	683	46.6	234	40.5
Weakly stratified	425	29.0	173	30.0
Strongly stratified	359	24.4	170	29.5
Total	1,467		577	

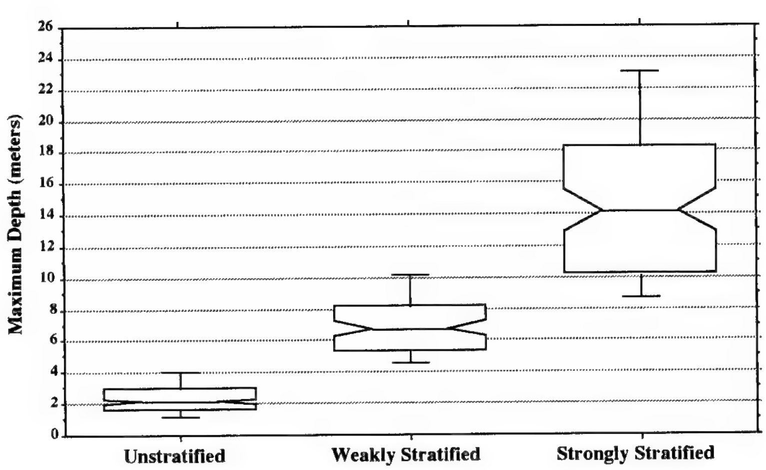

Fig. 1. Notched boxplots of median maximum depth in Adirondack Lake Survey Corporation brook trout lakes by stratification class.

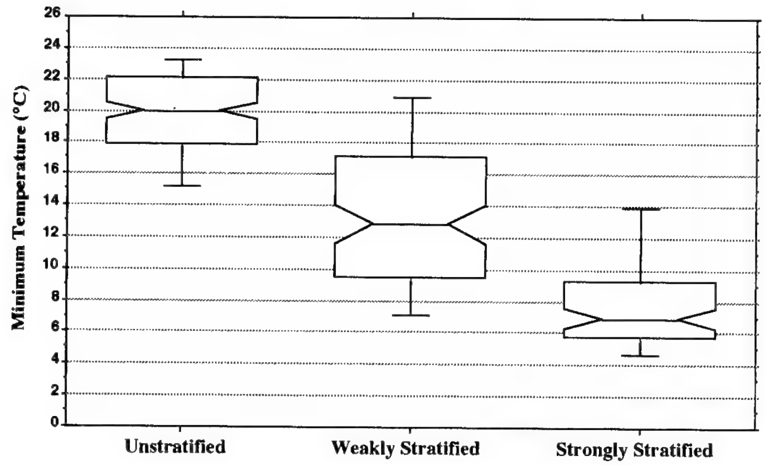

Fig. 2. Notched boxplots of median minimum summer water temperature in Adirondack Lake Survey Corporation brook trout lakes by stratification class.

Table 4. *Transparency, thermal classification, and water quality of Adirondack Fishery Research Program lakes during midsummer, 1979–90. S.S.-Strongly stratified; W.S.-Weakly stratified; Un.S.-Unstratified.*

Lake	Mean Secchi (meters)	Mean Kd (meters^{-1})	Thermal category a	Thermal category b	Summer surface pH (1979–90)
Canachagala	7.0	0.39	W.S.	W.S.	5.90–6.45
Chambers	2.0	0.96	S.S.	S.S.	5.35–6.08
Deer	3.5	0.72	Un.S.	Un.S.	5.43–6.40
Fourth Bisby	4.3	0.63	S.S.	S.S.	5.70–6.75
Goose	2.1	0.95	S.S.	S.S.	4.94–5.44
Green	5.5	0.50	S.S.	S.S.	5.84–7.10
Jones	8.2	0.30	Un.S.	W.S.	5.73–6.27
Mountain	5.1	0.54	W.S.	W.S.	5.89–7.19
Otter	4.0	0.67	S.S.	S.S.	4.94–5.92
Rock	4.8	0.57	Un.S.	Un.S.	5.70–6.00
Wheeler	2.8	0.83	Un.S.(50%) W.S.(50%)	Un.S.	5.85–6.60

[a]Thermal classification based on UFILS1 model.
[b]Thermal classification based on EPA temperature criteria.

The only inconsistencies were for Jones Lake and Wheeler Pond, which were borderline between unstratified and weakly stratified. Therefore, the UFILS1 model was used to classify the AFRP lakes. The five strongly stratified lakes were Chambers, Fourth Bisby, Goose, Green, and Otter; the two weakly stratified lakes were Canachagala and Mountain; and the four unstratified lakes were Deer, Jones, Rock, and Wheeler. There was general agreement in the thermal stratification classification of ELS lakes using the UFILS1 model and EPA criteria. As with the AFRP lakes, inconsistencies occurred only for lakes that were borderline between unstratified and weakly stratified—Mountain, Indigo, and Barto. The four strongly stratified lakes were Big Chief, Silver Dollar, Pocket, and Jones; the two weakly stratified lakes were Mountain and Highrock; and the three unstratified lakes were Trout, Indigo, and Barto.

Temporal Changes in Color, Transparency, and Thermal Stratification Patterns

The logistic model of stratification class for the ALSC lakes as a function of maximum depth and

Table 5. *Transparency, thermal classification, and water quality of Extensive Liming Study lakes during midsummer, 1983–86. S.S.–Strongly stratified; W.S.–Weakly stratified; Un.S.–Unstratified.*

Lake	Year	Mean Secchi (meters)	Mean kd (meters^{-1})	Thermal category a	Thermal category b	Summer surface pH (1983–86)
Big Chief	1983	5.5	0.49	S.S.	S.S.	4.80
	1984	3.4	0.74	S.S.	S.S.	5.05–5.24
	1985	3.75	0.68	S.S.	S.S.	5.14–5.46
	1986	2.5	0.87	S.S.	S.S.	4.57–4.90
Mountain	1983	8.0	0.31	Un.S.	Un.S.	4.67
	1984	5.5	0.49	W.S.	S.S.	6.20–6.50
	1985	7.6	0.34	Un.S.	W.S.	5.12–5.45
	1986	8.8	0.27	Un.S.	Un.S.	4.44–4.76
Highrock	1983	5.0	0.54	W.S.	—	5.07
	1984	4.0	0.44	W.S.	S.S.	6.75–6.76
	1985	5.5	0.49	W.S.	W.S.	6.14–6.24
	1986	6.2	0.65	W.S.	W.S.	4.92–5.15
Trout	1983	3.0	0.79	Un.S.	—	4.42
	1984	3.1	0.77	Un.S.	Un.S.	5.51–5.52
	1985	4.4	0.61	Un.S.	Un.S.	5.12–5.56
	1986	4.25	0.62	Un.S.	Un.S.	4.78
Silver Dollar	1984	2.5	0.87	S.S.	S.S.	4.20
	1985	2.8	0.82	S.S.	S.S.	4.86–5.40
	1986	1.8	0.99	S.S.	S.S.	4.12–4.45
Pocket	1984	2.75	0.83	S.S.	S.S.	4.31
	1985	2.8	0.82	S.S.	S.S.	4.54–5.44
	1986	2.0	0.96	S.S.	S.S.	4.07–4.34
Jones	1984	4.5	0.65	S.S.	S.S.	4.80
	1985	5.0	0.56	S.S.	S.S.	6.64–6.86
	1986	4.8	0.56	S.S.	S.S.	5.72–6.21
Indigo	1984	2.5	0.87	W.S.	W.S.	4.80
	1985	3.8	0.68	Un.S.	W.S.	6.63–6.77
	1986	4.9	0.55	Un.S.	Un.S.	5.68–6.12
Barto	1984	6.25	0.43	Un.S.	W.S.	4.55
	1985	5.6	0.46	Un.S.	Un.S.	6.85–6.87
	1986	5.8	0.48	Un.S.	Un.S.	4.26–4.99

[a]UFILS1 model.
[b]EPA criteria.

color indicates that relatively shallow lakes with low color have a high probability of being unstratified or weakly stratified and would be most sensitive to change in stratification class as a result of changes in water color (Fig. 3). Changes in color, transparency, and thermal stratification patterns observed in the LAMP and ELS lakes as a result of liming and reacidification illustrate this indication.

Increased dissolved organic carbon, decreased transparency, and a shift from weak to strong thermal stratification were documented for Woods Lake after liming in 1985 (Buckaveckas and Driscoll 1990). On the basis of estimated pre- and post-liming water color (color estimated from a regression function of dissolved organic carbon for ALSC lakes) in Woods Lake, the logistic model predicts the sensitivity of this low-color lake to changes in the intensity of thermal stratification resulting from relatively small shifts in water color (Fig. 4). Changes in transparency and thermal stratification class observed in the ELS lakes after lime applications also indicate that only low-color waters exhibited significant shifts in transparency

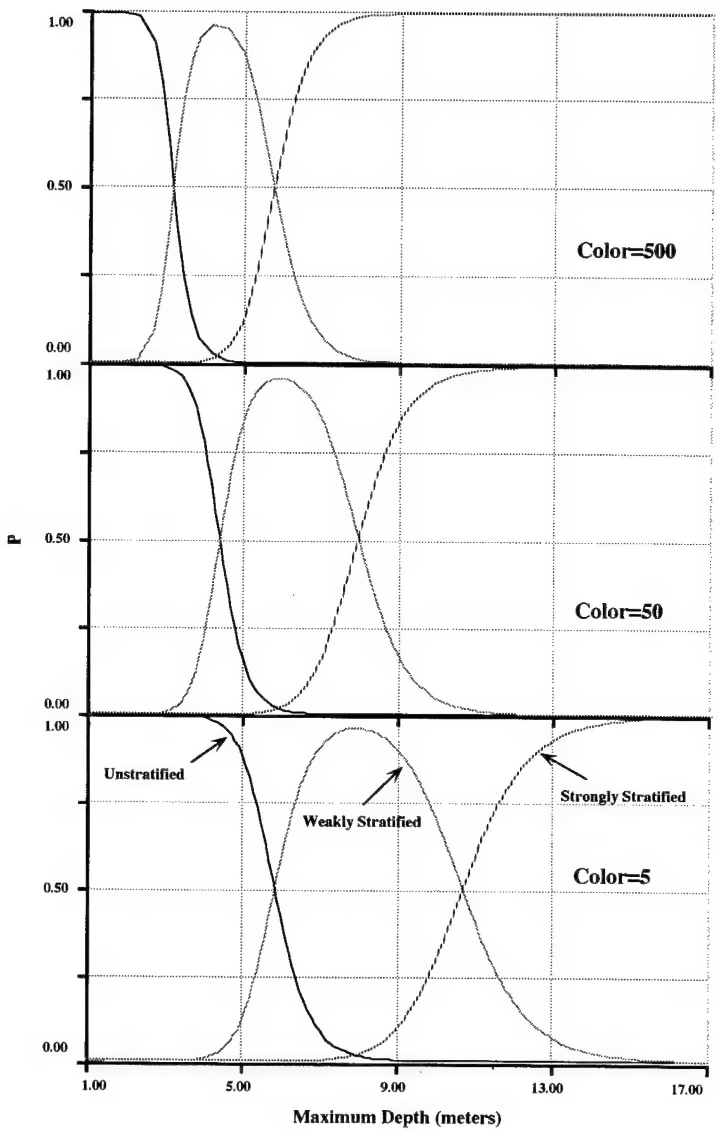

Fig. 3. Predicted probabilities of stratification for Adirondack Lake Survey Corporation lakes with water color 5, 50, and 500 as a function of maximum depth.

and thermal stratification patterns as a result of changes in acid–base status (Table 5). The low-color lakes included Mountain, Highrock, Trout, Jones, Indigo, and Barto. In these lakes, Secchi depths decreased immediately after lime applications. However, as these low-color lakes reacidified over 1–3 years, the Secchi depths in all waters except Barto Lake were greater than for preliming conditions. The high-color lakes included Big Chief, Silver Dollar, and Pocket. In these lakes, Secchi depths increased slightly after lime applications. As these high-color lakes reacidified over 1–3 years, the Secchi depths in all waters were less than in preliming conditions.

The effects of changes in color and transparency in Adirondack lakes on thermal stratification status that may have occurred as a result of long-term acidification were examined by using historical data for water color from Hinckley Reservoir (Schofield 1976). Hinckley Reservoir is a water supply impoundment for the city of Utica, New York, and receives the drainage of West Canada Creek in the southwest quadrant of the Adirondack region. Although Hinckley Reservoir is not acidic, about 35% of the ALSC lakes in this drainage system have pH levels less than or equal to 5. Weekly measurements of Hinckley water color obtained by the city of

Utica water treatment plant revealed a significant long-term trend of decreasing color from 1944 to 1975 (Fig. 5). Average August water color decreased 53% during this period. The effects of this magnitude of decrease in color on thermal stratification status of the ALSC lakes was assessed by comparing predicted stratification class frequencies calculated with the logistic model from present water color and color increased by the same magnitude of decrease in color observed in Hinckley Reservoir. This analysis indicates that this level of historical decrease in color would result in a significant increase in the proportion of unstratifed lakes (8%), a corresponding significant decrease in the proportion of strongly stratified lakes, and no significant change in the proportion of weakly stratified lakes (Fig. 6). Applying the same scenario of color change to lakes in the maximum depth range of 5–10 m (predominantly weakly stratified) results in greater proportional changes in stratification class frequencies (22% decrease in strongly stratified lakes) for these more sensitive transitional lakes (Fig. 7).

Seasonal Variation in Preferred Brook Trout Habitat

Coutant and Benson (1990) stated that "population fluctuations can be related to changes in the amount of habitat that is within the suitable bounds for a species, even though the linkage between habitat space and population size is not well quantified." In this investigation, the region between 10 and 16° C was considered preferred thermal habitat for brook trout. The size or volume of preferred thermal habitat in a lake is determined by the thickness of the preferred habitat zone (i.e., the vertical distance between the 10-

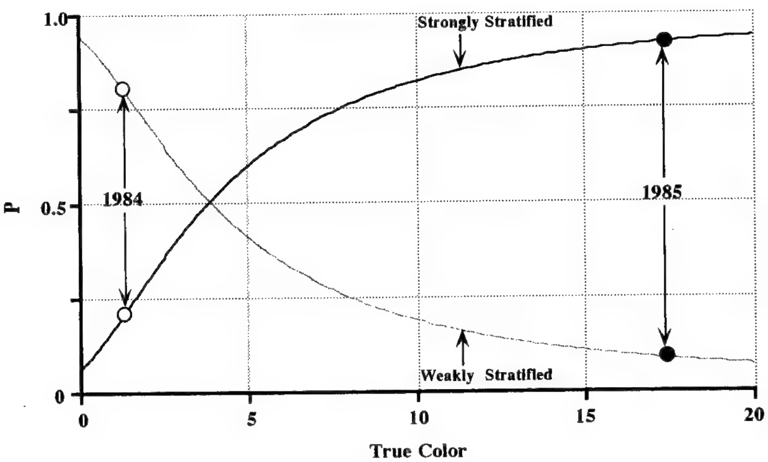

Fig. 4. Changes in predicted probabilities of stratification as a function of change in color of Woods Lake (maximum depth = 11 m), before (1984) and after liming (1985).

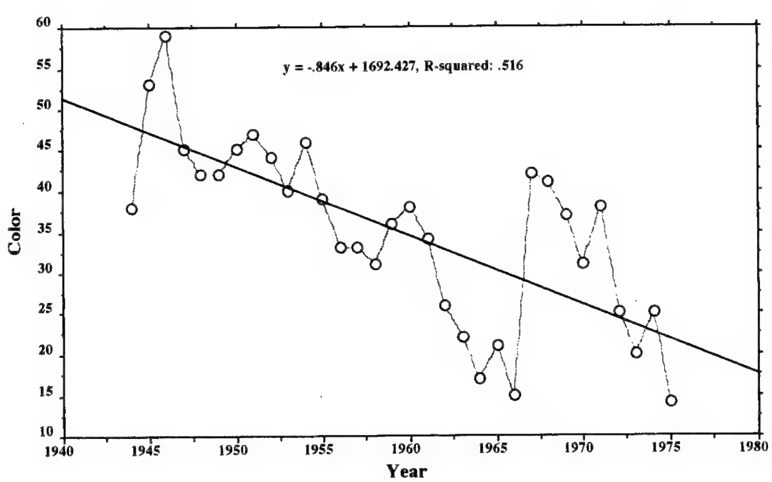

Fig. 5. Mean August water color (weekly observations) of Hinckley Reservoir from 1944 to 1975.

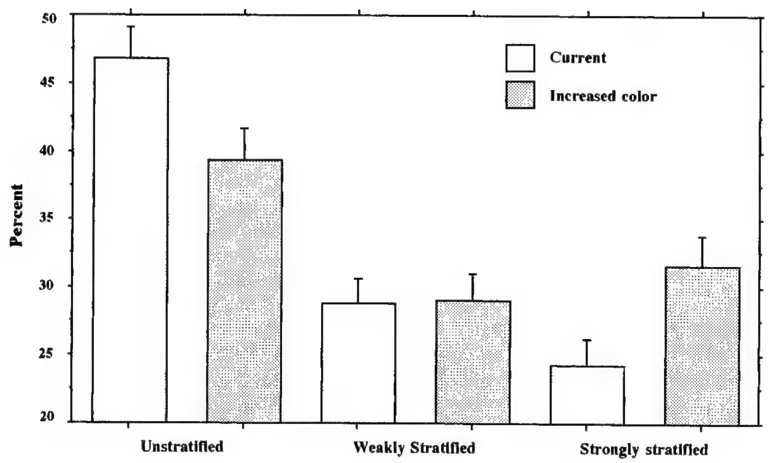

Fig. 6. Estimated distribution of Adirondack Lake Survey Corporation lakes among stratification categories based on currently observed color and increase in color proportional to trend in Hinckley Reservoir.

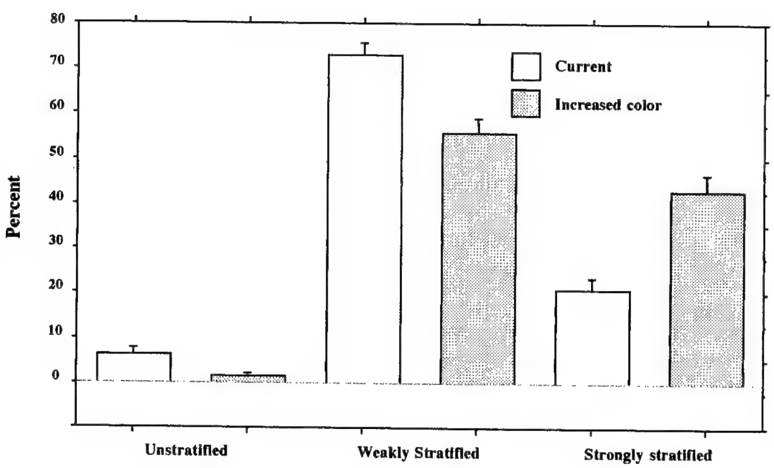

Fig. 7. Estimated distribution of Adirondack Lake Survey Corporation lakes (maximum depth 5–10 m) among stratification categories based on currently observed color and increase in color proportional to trend in Hinckley Reservoir.

and 16-degree isopleths), the location of the zone in the water column, and lake-dependent bathymetric features. The size of preferred habitat varies between lakes and fluctuates considerably seasonally and annually.

In Adirondack brook trout lakes, preferred thermal habitat usually becomes available in mid-April, with the spring warming of surface waters. As warming continues and surface waters exceed 16° C, the preferred habitat zone moves deeper in the water column. The depth of the preferred habitat zone continues to increase throughout summer, while the thickness of the zone decreases. With increasing depth and decreasing thickness, the volume of the preferred habitat zone decreases as a function of the bathymetry of the lake. The extent to which thermal habitat becomes limited in summer differs between lake types (e.g., stratified and unstratified) and is ultimately defined by individual lake characteristics.

Unstratified Lakes

In unstratified lakes, peaks in habitat availability occur in spring and fall, when the greatest percentage of the lake volume is within the preferred temperature range, as observed in Indigo Lake (Fig. 8). The critical period for brook trout occurs after the entire lake temperature rises above 16° C and until the temperature drops below 16° C in fall. During this period, no preferred habitat is available in the lake. The duration of the period without preferred habitat and the lake temperature for this period differs between lakes. Although brook trout can survive at temperatures higher than 16° C, growth rates would presumably be dictated by the length of time without

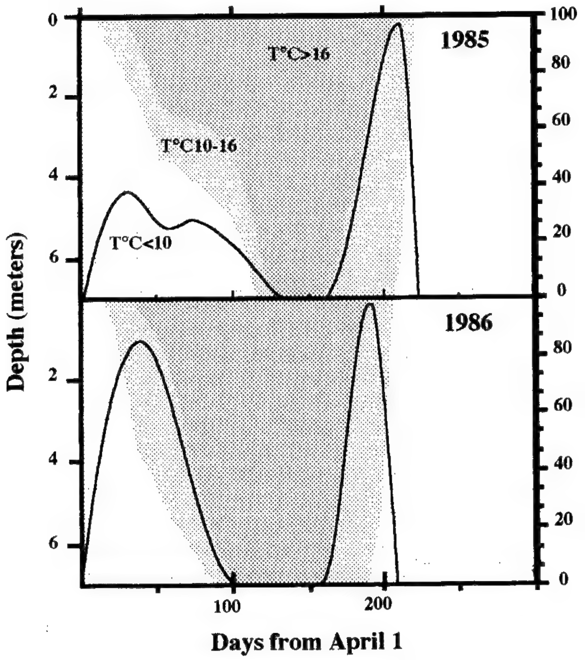

Fig. 8. Seasonal and annual variation in depth and volume (as percent of total lake volume) of preferred thermal habitat for brook trout (*Salvelinus fontinalis*) in Indigo Lake for two summers after liming.

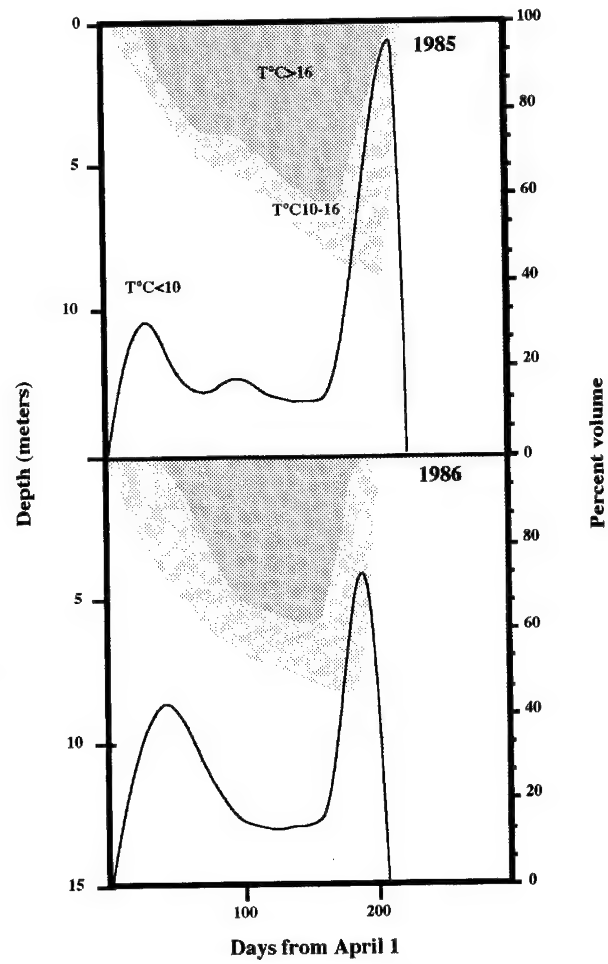

Fig. 9. Seasonal and annual variation in depth and volume (as percent of total lake volume) of preferred thermal habitat for brook trout (*Salvelinus fontinalis*) in Jones Lake for two summers after liming.

preferred habitat and the thermal environment during this period.

Stratified Lakes

Stratified lakes experience a peak in habitat availability in spring, although the percent volume is not as high as in unstratified lakes (Fig. 9). The volume of preferred habitat gradually diminishes as it is driven deeper into the water column with epilimnetic warming in summer. The most crucial time usually occurs in late August, when the preferred habitat volume is at a minimum. The relative volume of thermal habitat depends on its thickness and location in the water column and is lake specific. In some lakes the volume of suitable habitat is reduced further when the preferred thermal habitat intercepts oxygen-depleted hypolimnetic waters (Fig. 10). The maximum volume of habitat in stratified lakes is available in fall, soon after the critical summer period.

Annual Variation of Preferred Brook Trout Habitat

Variation in the thermal characteristics of lakes occurs from year to year, presumably due to annual variation in weather patterns. Meteorological parameters influence warming, cooling, and mixing rates of lakes and will directly affect brook trout habitat availability. In stratified lakes, the depth and thickness of the preferred thermal zone can fluctuate annually (Fig. 9). The minimum amount of preferred habitat is fairly consistent from year to year, but it seems that spring and fall peaks in habitat availability can fluctuate considerably. In lakes where hypolimnetic oxygen depletion is a concern, an increase in the depth of the preferred thermal zone can mean further restrictions in suitable habitat. In some instances, although suitable thermal habitat may occur in a lake, that habitat may be uninhabitable for brook trout because it all occurs in anoxic waters (Fig. 10). In unstratified lakes, the duration of time without suitable thermal habitat

seems to be influenced by weather patterns. Peaks in habitat availability in spring and fall are also influenced by annual weather changes (Fig. 8).

Thermal Habitat Changes After Liming

Long-term increases in light attenuation, or decreases in transparency, as a result of base addition have coincided with increases in dissolved organic carbon (DOC) and chlorophyll concentrations in Adirondack waters. Decreased thermocline depth, increased hypolimnetic volumes, and greater thermal stability have been associated with decreased transparency (Buckaveckas and Driscoll 1990).

Changes in the preferred brook trout thermal habitat of the LAMP lakes have occurred with liming. Before liming, Woods Lake and Cranberry Pond had extended periods during summer with little or no preferred thermal habitat available for brook trout (Figs. 11 and 12). In Woods Lake, less than 1% of the total lake volume was within the preferred thermal range for brook trout during the summer before liming. For the six summers that the water quality of Woods Lake has been maintained at suitable levels for brook trout survival by liming, the preferred thermal habitat volume has averaged 2.9%. In Cranberry Pond, where no preferred thermal habitat was available before liming, the minimum volume of preferred habitat in the first summer after liming was 8.5%. The duration of the fall peak in habitat availability seems

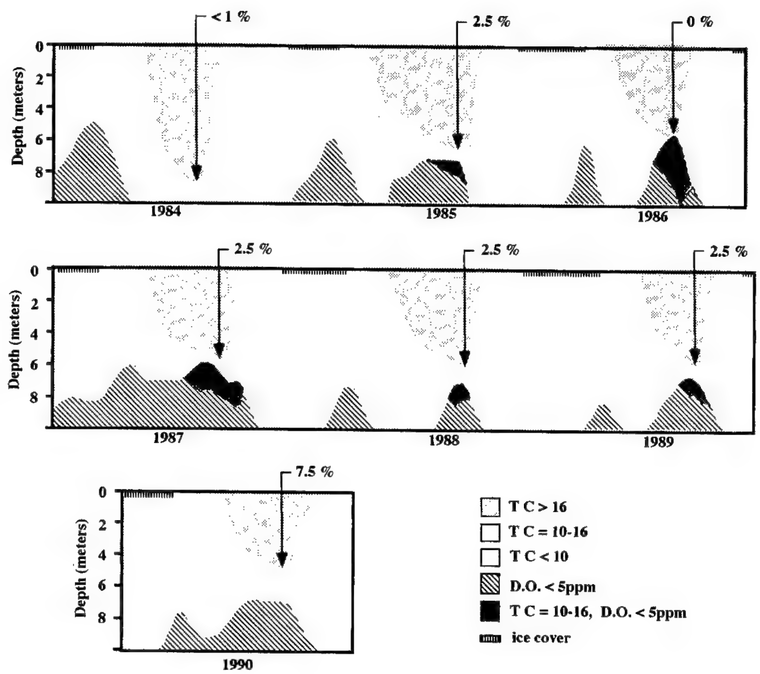

Fig. 10. Seasonal and annual variation of preferred brook trout (*Salvelinus fontinalis*) habitat in Woods Lake with minimum summer volumes as percent of the total volume.

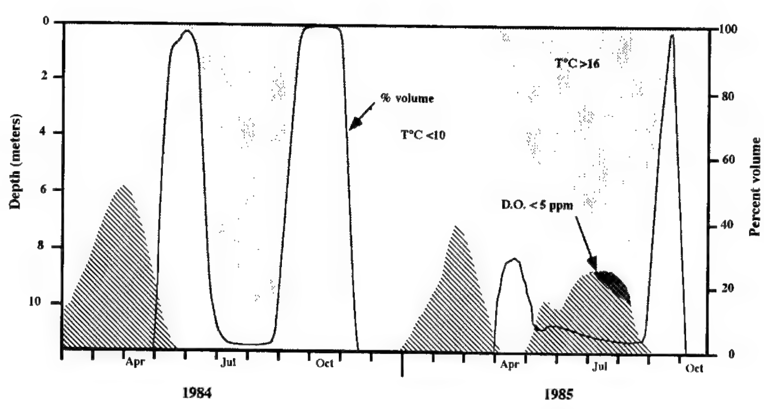

Fig. 11. Variation of depth and volume (as percent of total lake volume) of preferred brook trout (*Salvelinus fontinalis*) habitat before and after base addition in Woods Lake.

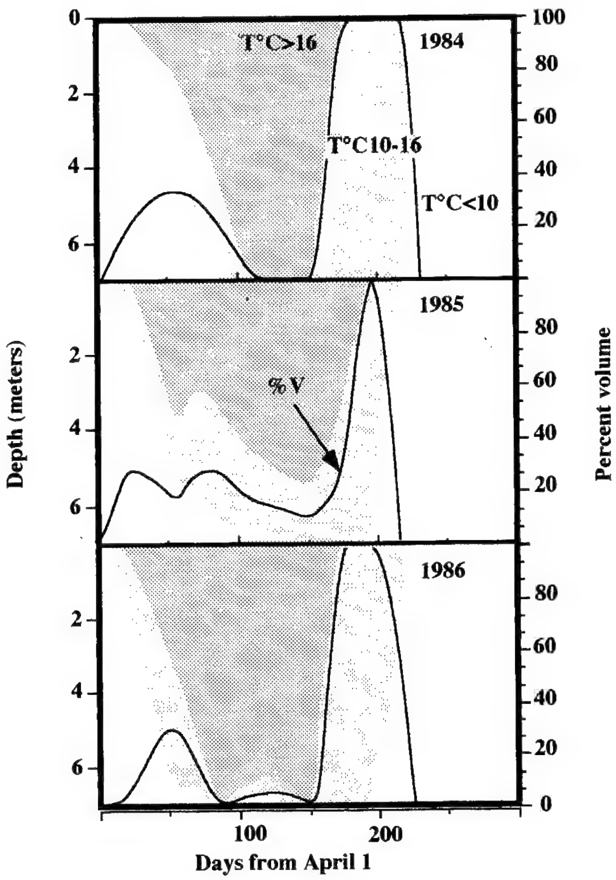

Fig. 12. Variation of depth and volume (as percent of total lake volume) of preferred brook trout (*Salvelinus fontinalis*) habitat for Cranberry Pond: 1984—preliming, 1985—postliming, and 1986—postreacidification.

to shorten after liming (Figs. 11 and 12). With increased hypolimnetic volumes the heat content of the lake is less, therefore less time is required for cooling in fall.

Summer hypolimnetic oxygen depletion, attributed to increases in thermal stability and phytoplankton productivity, has also been observed after liming of some lakes. In Woods Lake, habitat available for brook trout was reduced when preferred thermal regions and oxygen-depleted zones overlapped. As a result of this phenomenon, preferred habitat volume was reduced for five of six summers after liming and totally eliminated during the summer of 1986 (Fig. 10).

Thermal Habitat Changes After Reacidification of Limed Waters

Reacidification of limed waters is accompanied by reductions in DOC and chlorophyll, which are followed by a decrease in light attenuation or increase in transparency (Buckaveckas and Driscoll 1990). Increases in transparency were most apparent in Highrock and Mountain ponds as they were allowed to reacidify after liming in fall 1983 (Figs. 13 and 14). Highrock Pond had 16.9% of the total lake volume available as preferred thermal habitat for the first summer after liming. In the second and third summers after liming, Highrock Pond was reacidified, and the preferred thermal habitat was 4.5% and 3.7% (Fig. 15). Cranberry Pond went from 8.5% of the total lake volume available as preferred habitat for the first summer after liming to having no available thermal habitat after reacidification (Fig. 12).

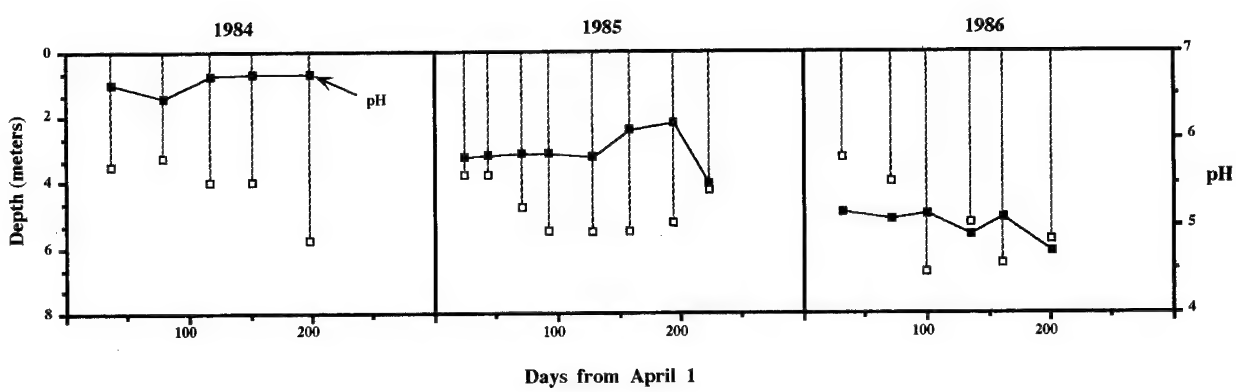

Fig. 13. Secchi depths and surface pH readings for Highrock Pond.

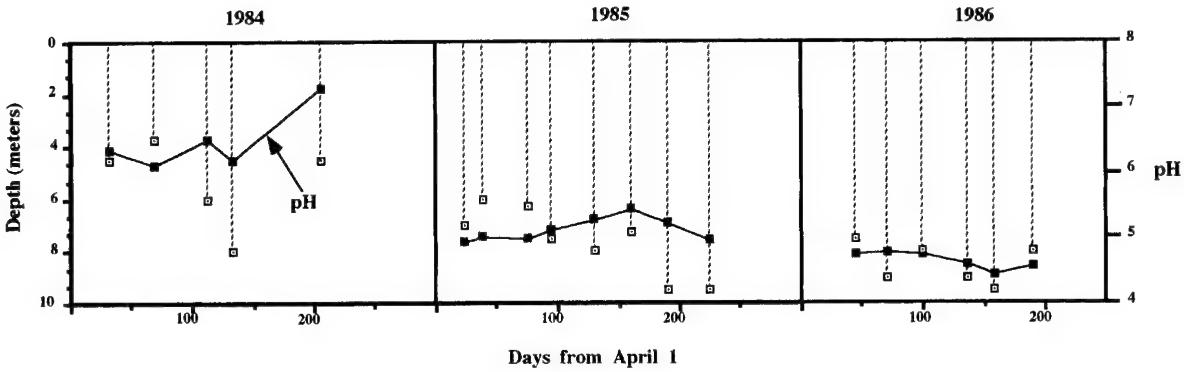

Fig. 14. Secchi depths and surface pH readings for Mountain Pond.

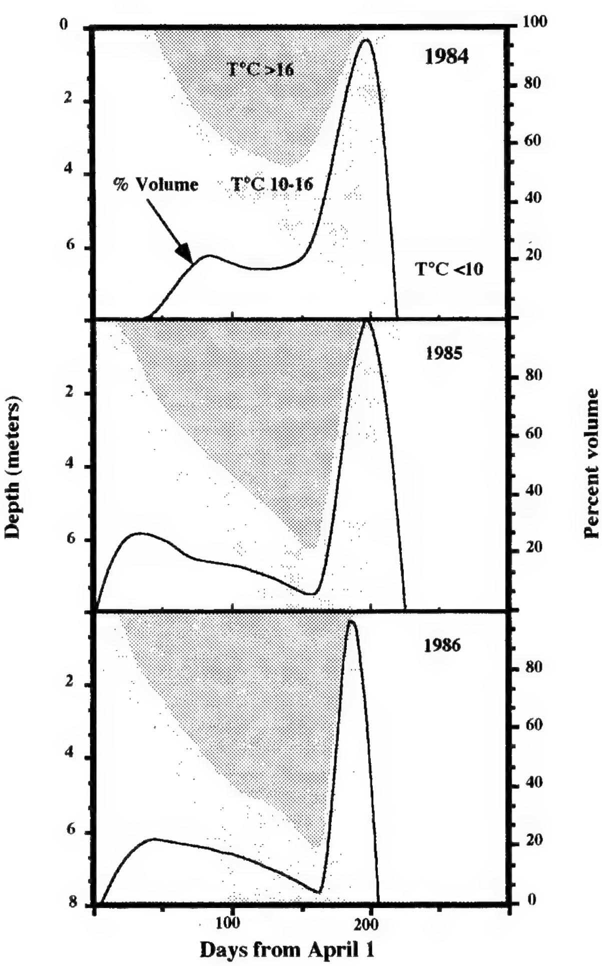

Fig. 15. Seasonal and annual variation in depth and volume (as percent of total lake volume) of preferred thermal habitat for brook trout (*Salvelinus fontinalis*) in Highrock Pond for three summers after liming.

Comparisons of Brook Trout Growth by Stratification Class

Comparisons of mean weight at age (ages 1–3) for ALSC brook trout populations in unstratified, weakly stratified, and strongly stratified lakes did not reveal any consistent significant differences ($P < 0.05$) between populations sampled in weakly stratified lakes and either strongly stratified or unstratified lakes. As a result of this preliminary comparison all subsequent comparisons were restricted to unstratified and strongly stratified lakes. Previous analyses of brook trout growth in ALSC lakes (Schofield 1990) indicated that the average size of brook trout sampled in lakes with natural reproduction was significantly less than in lakes maintained by stocking, presumably as a result of higher population densities and intraspecific competition for food in the lakes supporting natural reproduction. For this reason, presence or absence of natural reproduction was included, in addition to season sampled, as an additional factor in ANOVA comparisons of mean weight at age for the ALSC lakes. These comparisons of mean weight at age (Table 6) revealed a significant effect of season only at age 1, significantly greater mean weights at all ages for populations without natural reproduction, and significantly greater mean weights in strongly stratified lakes at ages 2 and 3. Examination of the trends in F values for these comparisons by age indicates decreasing significance of season and natural reproduction effects with increasing age and increasing significance of stratification effect with increasing age (Table 6).

The mean weight at age of brook trout in the AFRP lakes was determined for the three thermal categories. The mean weights for ages 1+ through

4+ in AFRP lakes from 1979–90 is summarized in Table 7. Comparisons (ANOVA, $P < 0.05$) of mean weights between strongly stratified and unstratified AFRP lakes showed no significant differences at age 1+ to 4+ for the two lake types. Small sample size, in conjunction with widely varying forage sizes and densities, probably contributed significantly to the wide range of growth observed between these lakes, particularly for ages 3+ and 4+ fish. Brook trout growth is provided for all AFRP lakes classified as strongly stratified (Appendix Table 1), weakly stratified (Appendix Table 2), and unstratified (Appendix Table 3). The best observed growth occurred in lakes with a fish or crayfish forage base present. This includes the three lake types as follows: strongly stratified (Fourth Bisby Lake—mudminnows, Green Lake—pumpkinseed sunfish), weakly stratified (Ca-

Table 6. *Comparison of the effects of season captured, presence or absence of natural reproduction, and stratification on mean weights (log transformed in ANOVA) at age for brook trout sampled in Adirondack Lake Survey Corporation lakes.*

Age	Season			Natural reproduction			Stratification		
	Spring		Fall	Present		Absent	Stratified		Unstratified
I									
Mean	66.2		94.8	69.8		89.7	83.2		75.5
F		30.42			15.23			2.12	
$P > F$		0.0000			0.0001			0.1468	
$N = 302$									
II									
Mean	186.6		209.9	179.5		218.3	210.4		186.2
F		3.67			10.53			3.82	
$P > F$		0.0562			0.0013			0.0516	
$N = 302$									
III									
Mean	378.4		434.5	372.4		441.6	458.1		358.9
F		3.54			5.27			10.51	
$P > F$		0.0615			0.0230			0.0014	
$N = 172$									

Table 7. *Observed brook trout growth in Adirondack Fishery Research Program lakes by thermal stratification categories from fall trapnet samples during 1979–90.*

Stratification class	Age (years)	Sample size (*n*)	Mean length (millimeters)	Mean weight (grams)
Stongly stratified				
	1	1,947	262.8	184.1
	2	584	324.8	366.3
	3	83	364.9	533.6
	4	13	402.8	742.6
Weakly stratified				
	1	1,258	278.3	223.4
	2	635	345.1	430.5
	3	82	380.5	528.3
	4	35	396.4	759.5
Unstratified				
	1	1,134	243.1	136.7
	2	272	311.2	328.0
	3	115	353.4	503.1
	4	14	365.8	505.4

nachagala Lake—crayfish), and unstratified (Rock Lake—crayfish) lakes. Poorer growth occurred in the three lake types with only a macroinvertebrate forage base present as follows: strongly stratified (Chambers Lake, Goose Lake, Otter Lake), weakly stratified (Mountain Pond), and unstratified (Deer Lake, Jones Lake, Wheeler Pond). The observed growth was generally poorest in unstratified lakes when stocked at high densities. Sustained good growth past age 2+ was observed in AFRP lakes with a diverse forage base (including larger prey items such as crayfish and minnows), whereas growth was generally poorer in lakes lacking larger prey items (Fig. 16). These observations indicate that lack of preferred summer thermal habitat can be compensated for by the presence of larger prey items, within the range of stocking densities examined.

The mean weight at age of brook trout in the ELS lakes was determined for the three thermal categories. The growth of the first and second year classes stocked after liming were determined for ages 1+ and 2+ fish. Size at stocking was comparable in 1983 (mean weight, 57.8 g) and 1984 (mean weight, 57.1 g), but smaller fish were stocked in 1985 (mean weight, 29.8 g). The observed differences in growth between the first and second year classes stocked after liming included a pooled comparison between 1983 and 1984 year classes (Group I ELS lakes) and 1984 and 1985 year classes (Group II ELS lakes). Observed differences in growth between the first two year classes stocked after liming (pooled mean difference = 108.4 g) were significantly greater than the differences in size at stocking (largest difference = 28.0 g). The observed brook trout growth in ELS lakes from 1983 to 1986 is summarized in Table 8. The ELS lakes had been fishless for several years or had never had fish populations. The lakes were characterized by an abundant forage base of macroinvertebrates before lime applications. Comparisons (ANOVA, $P < 0.05$) of mean weight

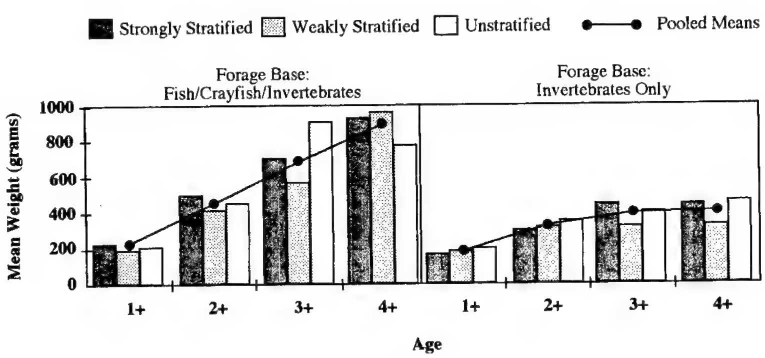

Fig. 16. Comparison of brook trout (*Salvelinus fontinalis*) growth in Adirondack Fishery Research Program lakes by stratification category and forage base type.

Table 8. *Observed brook trout growth in Extensive Liming Study by thermal stratification categories, for the first and second year classes stocked after lime application; from fall trapnet samples during 1984–86.*

Thermal category	Age (years)	Sample size (*n*)	Mean length (millimeters)	Mean weight (grams)
First year class				
Strongly stratified	1	257	282.7	229.3
	2	44	306.3	285.9
Weakly stratified	1	329	287.3	274.3
	2	51	309.2	276.8
Unstratified	1	413	305.2	304.3
	2	29	325.4	332.0
Second year class				
Strongly stratified	1	76	253.6	160.3
Weakly stratified	1	26	253.7	159.2
Unstratified	1	97	250.3	163.2

between strongly stratified and unstratified ELS lakes showed (1) significantly greater growth, for the first year class stocked after liming, in unstratified versus stratified lakes at ages 1+ and 2+; and (2) no significant difference in growth, for the second year class stocked after liming, in unstratified versus stratified lakes at age 1+. These results indicate that the lack of preferred thermal habitat did not limit the growth of age 1+ fish in unstratified ELS lakes. On the basis of these analyses, temperature did not seem to be the primary regulator of growth in the AFRP and ELS lakes for age 1+ fish.

Evaluation of Brook Trout Growth in Relation to Preferred Thermal Habitat, Stocking Density, and Prey Density

Table 9 provides the best fit regression models for the relation between mean weight at age and preferred thermal habitat and stocking density. Simple regression, multiple regression, and stepwise regression statistics ($P < 0.05$) consistently identified cumulative stocking density (*X4*) as the significant variable related to the log transformed mean weight (*Y1*). Appendix Tables 4 through 7 provide results from the described regression screening evaluations for ages 1+ to 4+ fish. Simple regression models, for all ages, that included the cumulative stocking (*X4*) variable, accounted for the most variation (i.e., greatest R^2) in observed mean weight (*Y1*) in fall samples. The R^2 values increased as the age of the fish increased. Although significant relations ($P < 0.05$) were detected between mean weight (*Y1*) and volume of preferred thermal habitat (*X1*), the variation accounted for by the model was low (R^2 values <0.2).

Bioenergetic Analysis of Thermal Stratification Effects on Brook Trout Growth

Maintenance temperatures for brook trout weighing 400–1,000 g and feeding on prey with energy contents of 0.7–3.0 cal per organism at a constant biomass of 1 cal/m^3 were determined by using the Kerr (1971) growth model (Fig. 17). The range of prey sizes employed in this simulation are representative of invertebrate prey eaten by brook trout in Adirondack lakes, and the prey biomass level is typical for unproductive Adirondack waters (Evans 1989; Gloss et al. 1989b). A typical prey

Table 9. *Best regression models for relations between mean weight, preferred thermal habitat, and stocking density in Adirondack Fishery Research Program lakes for ages 1+ through 4+ brook trout.*

Type	Model	Adjusted R^2
Age 1+		
Simple regression:	$\ln(Y1) = 5.486 - (0.003)X4$	0.293
Multiple regression:	None	
Stepwise regression:	Excluded *X1* and *X2* in all cases.	
Age 2+		
Simple regression:	$\ln(Y1) = 6.332 - (0.003)X4$	0.563
Multiple regression:	None	
Stepwise regression:	Excluded *X1* and *X2* in all cases.	
Age 3+		
Simple regression:	$\ln(Y1) = 6.724 - (0.002)X4$	0.695
Multiple regression:	$\ln(Y1) = 6.634 + X1 - (0.008)X3$	0.610
Stepwise regression:	Included *X1* with *X3*.	
Age 4+		
Simple regression:	$1n(Y1) = 6.974 - (0.002)X4$	0.740
Multiple regression:	None	
Stepwise regression:	*X1* and *X2* excluded in all cases.	

Dependent variable
Y1 = mean weight (grams)
Independent variables
X1 = volume preferred habitat (m^3)
X2 = percent volume preferred habitat (%)
X3 = stocking density (pounds/ha)
X4 = cummulative stocking density (pounds/ha)

item with an energy content of 0.7 cal would be a chironomid larva, whereas a large odonate nymph could contain 2–3 cal. The curves for maintenance temperature as a function of fish weight (Fig. 17) indicate that brook trout inhabiting unstratified lakes with high summer water column temperatures would require a diet of relatively large prey to attain weights in excess of 500–600 g. In stratified lakes, where brook trout would have access to lower water temperatures, fish of larger size could be produced with less energy expenditure by feeding on smaller prey with lower energy content. Simulation of the effects of increasing either prey size or prey density, to achieve an equivalent increase in prey biomass, indicates that larger fish (>500–600 g) would be able to maintain their body weight more efficiently by feeding on larger prey, rather than more numerically dense prey at the same biomass (Fig. 18). It should also be noted that smaller brook trout (e.g., 100–400 g) have a relatively high maintenance temperature for the ranges of prey size and density simulated in Fig. 18.

The hypothesized requirement of large prey to produce large brook trout in warm, unstratified waters was further assessed by examining the characteristics of ALSC lakes where relatively large brook trout (≥1,000 g maximum weight) were captured (N = 35). Large potential prey,

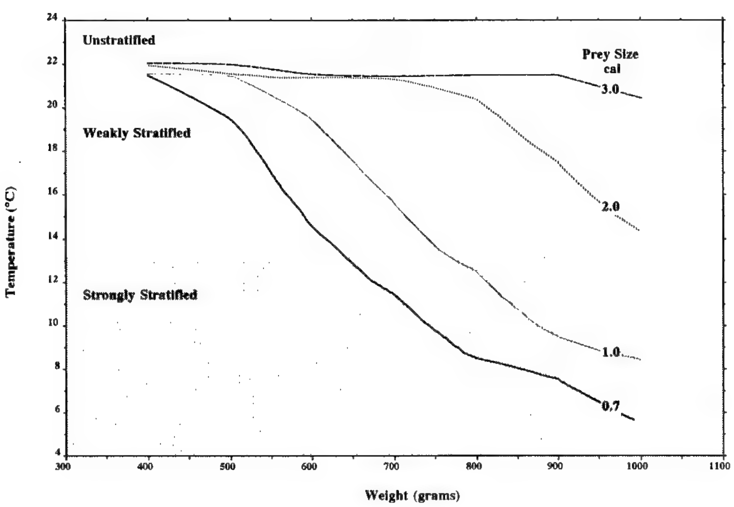

Fig. 17. Estimated maintenance temperatures for brook trout (*Salvelinus fontinalis*) feeding on prey of 0.7–3.0 cal at a constant prey biomass of 1 cal/m^3. *Shaded* zones represent median minimum summer temperature limits for stratification categories.

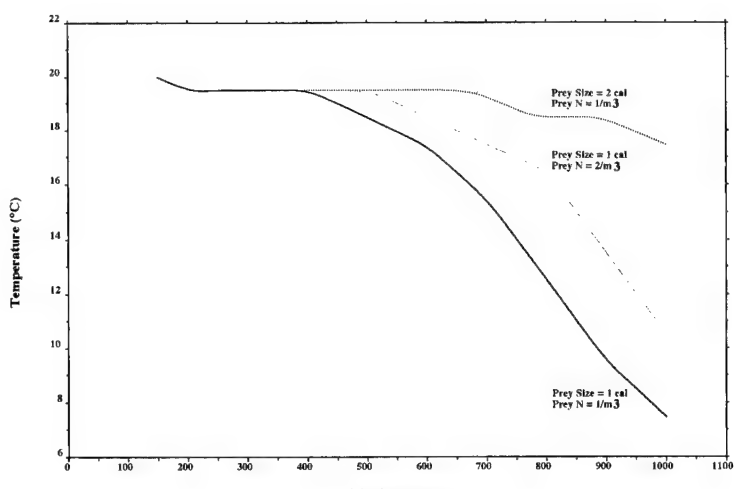

Fig. 18. Simulated effects of doubling either prey size or prey density on brook trout (*Salvelinus fontinalis*) maintenance temperatures as a function of fish size.

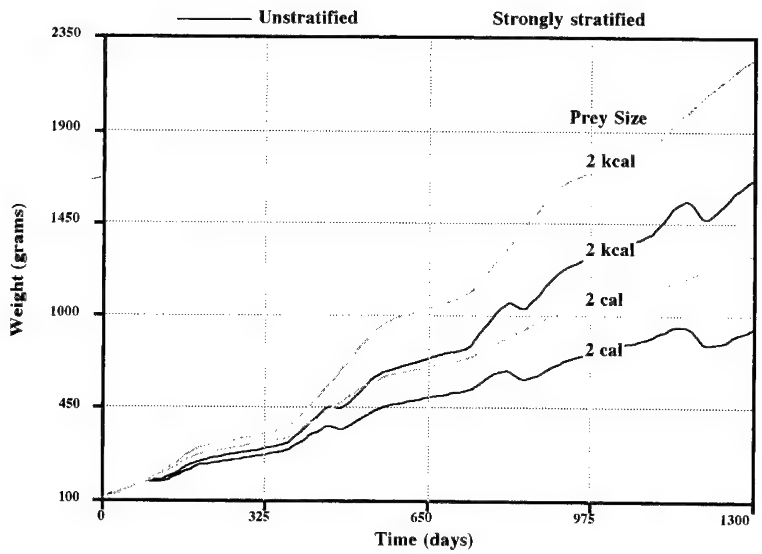

Fig. 19. Simulated growth in weight of brook trout (*Salvelinus fontinalis*) in strongly stratified and unstratified lakes on diets of minnows (prey size 2 kcal, density 0.2 cal/m^3) or invertebrates (prey size 2 cal, density 2 cal/m^3).

represented by small cyprinid fish species, were present in all of the unstratified lakes with large brook trout (N = 12). However, in the 23 stratified lakes with large brook trout 6 lakes (26%) did not contain large prey (either cyprinids or naturally reproduced young-of-year brook trout) and the fish must have attained large size entirely on an invertebrate diet. Model simulations of brook trout growth in strongly stratified and unstratified lakes, with representative diets of either large (cyprinids) or small (invertebrate) prey, indicate that trout feeding on large prey could easily attain weights in excess of 1,000 g in either lake type. However, trout restricted to an invertebrate diet would be able to attain weights in excess of 1,000 g only in strongly stratified lake types, where access to lower water temperatures is available (Fig. 19).

Simulations of brook trout growth were conducted over a 4-year period for yearling cohorts with an initial weight of 100 g in unstratified, weakly stratified, and strongly stratified lakes, with equal prey size and density, for comparison of relative differences in mean weights at age and evaluation of preferred temperatures. Representative monthly minimum and maximum temperatures available to the fish in each lake type are shown in Fig. 20. Iterative comparisons of daily growth rates at temperature intervals of 1 Celsius degree across the available temperature range were performed during the simulations to select the temperature that maximized growth. Preferred temperatures approximated the minimum summer temperatures available in the unstratified lake simulation and fish lost weight at age 2 and greater during periods when summer temperatures were high (Fig. 21). In the weakly stratified and strongly stratified lake types, fish selected progressively lower summer temperatures with increasing age and size to maintain maximum growth rates (Figs. 22 and 23). Comparison of growth for the three lake types reveals an increasing differential in weight at age between the unstratified and stratified lake types with increasing age beyond age 2 (Fig. 24). Increasing prey size in the unstratified lake by a factor of 2 to 3 is sufficient to partially compensate for the lack of preferred summer thermal habitat (Fig. 25). Although average weight at age is increased in the unstratified lake by increasing prey size, high summer temperatures still result in temporal negative growth phases.

Discussion

Ferguson (1958) stated that temperature acting alone can influence fish response in the laboratory, but many other factors can interfere with the expression of response to temperature in natural environments. In the relatively unproductive lakes of the Adirondack region intraspecific competition for limited prey resources can lead to density-dependent growth, particularly in naturally reproducing brook trout populations with high rates of recruitment. In this study, Adirondack lakes were classified as strongly stratified, weakly stratified, or unstratified (Linthurst et al. 1986; Driscoll et al. 1990), based on midsummer thermal struc-

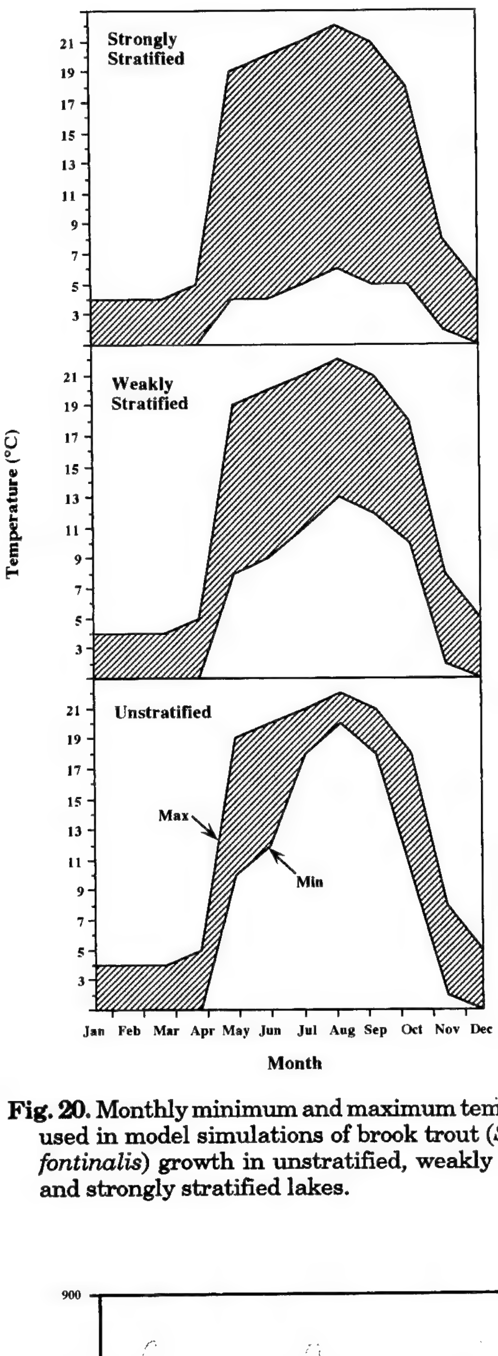

Fig. 20. Monthly minimum and maximum temperatures used in model simulations of brook trout (*Salvelinus fontinalis*) growth in unstratified, weakly stratified, and strongly stratified lakes.

ture. Comparisons of mean weight at age between strongly stratified and unstratified AFRP lakes showed no significant differences between the two lake types. Small sample size, in conjunction with widely varying forage sizes and densities, probably contributed significantly to the wide range of growth observed between these lakes. Comparisons between strongly stratified and unstratified ELS lakes showed significantly greater growth, by the first year class stocked after liming, in unstratified versus stratified lakes at ages 1+ and 2+ and no significant difference in growth, by the second year class stocked after liming, in unstratified versus stratified lakes at age 1+. These results indicate that the lack of preferred thermal habitat did not limit the growth of age 1+ fish in unstratified ELS lakes. On the basis of these analyses, density-dependent factors rather than temperature seemed to be the primary regulator of growth in the AFRP and ELS lakes for young fish. Simple regression analysis between log transformed mean weight at age and the minimum observed volume of preferred thermal habitat in AFRP lakes showed no significant relation for age 1+ fish, and significant positive relations for ages 2+, 3+, and 4+ fish. Although there were significant positive relations, the adjusted R^2 values for age 2+ (0.101), age 3+ (0.186), and age 4+ (0.173) fish demonstrate that only a small amount of the observed variation in growth was accounted for by the minimum volume of preferred thermal habitat. The analysis indicates that proportionally more variation in growth is accounted for by thermal habitat conditions in the older, larger fish. Similar results were obtained in analyses of the ALSC lakes, and this larger data base also revealed highly significant thermal stratification effects on growth of older (ages 2 and 3) brook trout.

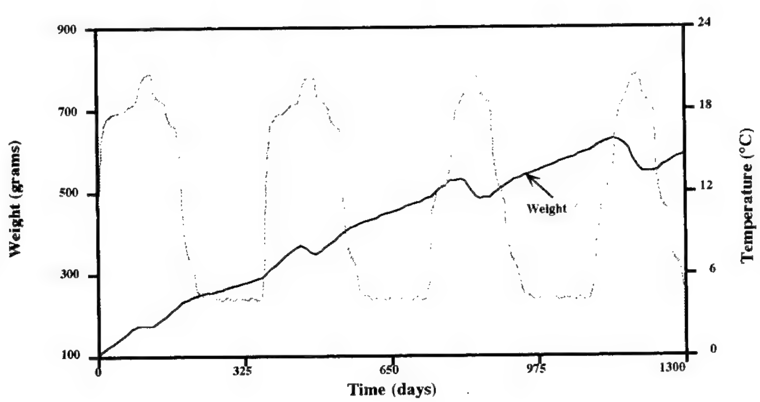

Fig. 21. Simulated preferred temperature and growth in weight of yearling brook trout (*Salvelinus fontinalis*) in an unstratified lake. *Shaded* area represents seasonal maximum–minimum temperatures available to the fish. Prey size (1 cal) and prey density (1 cal/m^3) constant.

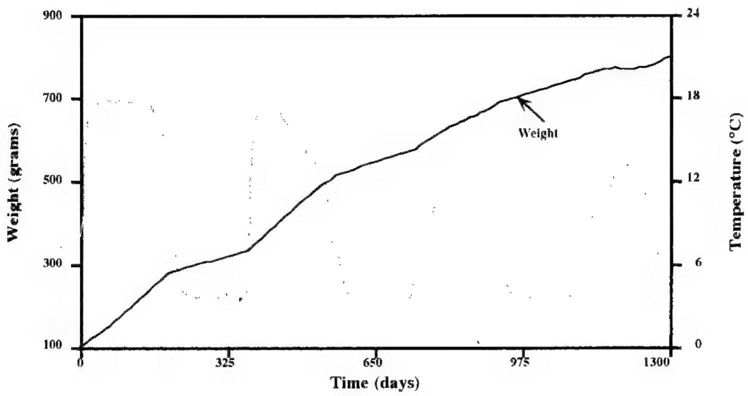

Fig. 22. Simulated preferred temperature and growth in weight of yearling brook trout (*Salvelinus fontinalis*) in a weakly stratified lake. *Shaded* area represents seasonal maximum-minimum temperatures available to the fish. Prey size (1 cal) and prey density (1 cal/m^3) constant.

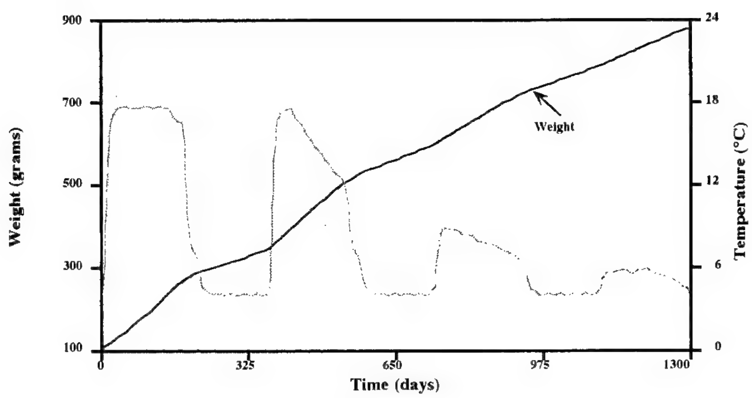

Fig. 23. Simulated preferred temperature and growth in weight of yearling brook trout (*Salvelinus fontinalis*) in a strongly stratified lake. *Shaded* area represents seasonal maximum-minimum temperatures available to the fish. Prey size (1 cal) and prey density (1 cal/m^3) constant.

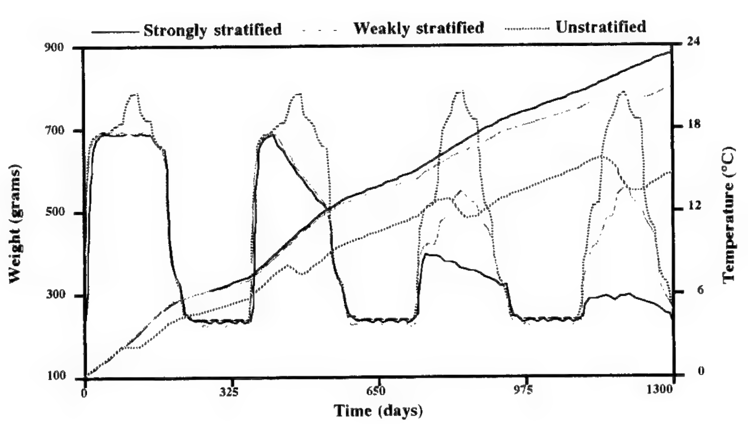

Fig. 24. Simulated preferred temperatures and growth in weight of yearling brook trout (*Salvelinus fontinalis*) in strongly stratified, weakly stratified, and unstratified lakes. Prey size (1 cal) and prey density (1 cal/m^3) constant.

The presence or volume of preferred thermal habitat during midsummer seemed to have the least effect on the growth of age 1+ fish. Yearling brook trout, with unrestricted rations, have been shown to have an optimal range for growth in temperatures of 10 to 19° C (Hokanson et al. 1973). The significantly greater growth of brook trout in unstratified versus stratified ELS lakes and the

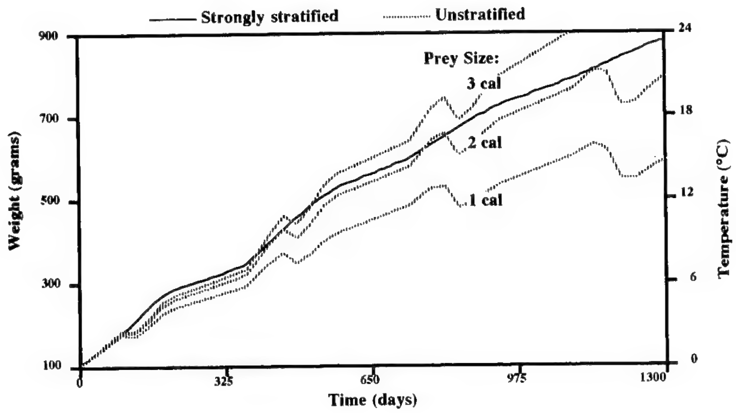

Fig. 25. Simulated growth in weight of yearling brook trout (*Salvelinus fontinalis*) in a strongly stratified lake (prey size 1 cal) and unstratified lake (prey size 1–3 cal). Prey density (1 cal/m^3) constant.

lack of significant differences in mean weight at age 1+ between stratification categories in the ALSC lakes strongly indicates that high temperatures (>19° C) had no negative effect on growth of young fish in unstratified lakes. Fall yearling brook trout generally range from 150 to 300 g, and, as judged from model simulations of maintenance temperature, temperatures to 20° C would not result in negative growth efficiency.

The presence or volume of preferred thermal habitat in midsummer accounted for some of the observed variation in growth for age 2+ and older fish. Larger fish have increasingly higher metabolic demands, which are exacerbated by high (>16° C) water temperatures. Laboratory studies provide sufficient evidence that brook trout prefer a thermal range of 10–16° C (MacCrimmon and Campbell 1969; Coutant 1977), with a final preferendum of 15.5–16.8° C (Cherry et al. 1977). Further, brook trout suffering starvation have been shown to select temperatures of 14.5 to 16.0° C (Javaid and Anderson 1967), representing an attempt to conserve energy. Other strategies to conserve energy under starvation conditions include decreased oxygen consumption (Beamish 1964), reduced spontaneous activity (Beamish 1964), and reduced standard metabolic rate (Javaid and Anderson 1967). These energy conservation strategies, under starvation conditions, would be most pronounced for larger fish (>600 g) at temperatures exceeding 19° C.

Model simulations of brook trout growth in unstratified and stratified lakes were qualitatively consistent with observed differences in mean weights at age observed in the ALSC unstratified and stratified lakes. An increasing differential in mean weights at age, beyond age 2, between the unstratified and stratified lakes was evident in the model simulations and the observed ALSC data. This analysis also indicates that, for given levels of prey biomass in unproductive waters, sustained growth beyond an approximate threshold of 500 to 600 g body weight requires the availability of increasingly cooler water that would only be available in stratified lakes during summer periods. In the model simulations, age 2 and older brook trout "moved" to increasingly cooler waters in the stratified lake scenario to maximize growth rate. Limited field studies indicate that brook trout will select midsummer temperatures approaching their final preferendum of 15.5–16.8° C, if that thermal habitat is available. Cone (1987) found that brook trout were located in temperatures of 10 to 15° C, near the bottom, in an Adirondack pond. Lackey (1970) described brook trout distribution with a distinct increase in depth of capture to 25 feet during midsummer in Echo Lake, Maine, but could not establish a clear relation between distribution and either temperature or dissolved oxygen. Haraldstad and Jonsson (1983) provided a detailed account of brown trout distribution during midsummer in a Norwegian lake. Most age 1+ and 2+ fish were restricted to the littoral zone, while larger, older fish occupied the pelagic and deeper benthic habitats with cold water. These extremely limited field observations of trout distribution in ponded waters suggest a general trend of larger trout seeking out deeper, colder (≤16° C) water. This is reasonably attributed, in part, to temperature, considering the higher metabolic costs to larger (>600 g) fish in warm (higher than 16° C) waters. Movement to deeper, colder water would reduce metabolic costs while allowing fish to periodically move into shallow waters to forage. This may explain the presence of large fish in both shallow and deep areas of Echo Lake (Lackey 1970) during summer. Smaller fish do not necessarily need to move into

colder water, if food is available in littoral areas, to maintain positive growth. The fish most vulnerable to warming waters in excess of 16° C would be those larger than 600 g, which represents age 2+ and older brook trout in Adirondack waters.

The rapid growth of age 1+ brook trout in ELS lakes, immediately after base additions, provides evidence of a significant effect on the forage base by fall fingerling brook trout (Schofield et al. 1986; Gloss et al. 1989a). During their first year of growth, fall fingerlings compose the largest proportion of stocked brook trout populations. Because age 1+ fish can occupy a wider thermal range (10–19° C) and sustain optimal growth with adequate forage (Hokanson et al. 1973), they can successfully forage in the littoral zone throughout the midsummer period. Larger brook trout require more food to maintain positive growth, dependent on the available temperatures they can occupy.

Regression analysis identified a significant relation between mean weight and cumulative stocking density of fall fingerlings. In AFRP lakes, the amount of variation in observed growth accounted for by cumulative stocking density increased as age increased for age 1+ R^2 = 0.293), age 2+ R^2 = 0.563), age 3+ R^2 = 0.695), and age 4+ R^2 = 0.740) fish. When stocking density increases, the forage base may decrease resulting in less available prey. This creates a density-dependent effect that seems to have a primary role in regulating growth in the AFRP lakes. Density-dependent growth has been identified for the ELS lakes (Gloss et al. 1989a). As expected, the effects of a reduced forage base will have the greatest effect on larger fish with higher metabolic demands, particularly if preferred temperatures are not available.

Density-dependent growth is a well-established paradigm that is reflected in the recommended stocking rates for Adirondack brook trout lakes. New York State Department of Environmental Conservation stocking rates are based on the morphoedaphic index and range from 20 to 70 fish / ha (Engstrom-Heg 1979). The recommended stocking rate for newly limed Adirondack lakes is 40 fish / ha (Gloss et al. 1989a). The stocking rates in the AFRP (20–75 fish / ha) and the ELS (about 40 fish / ha) lakes generally fell within those prescribed stocking rates. It is difficult to fully assess the effect of stocking density on growth since most stocking rates were less than 50 fish / ha and considerably lower for most stratified lakes. Another limitation is a general lack of age 3+ and older brook trout in most Adirondack lakes. Factors affecting growth of these larger fish, such as temperature and predator–prey densities, are difficult to assess with the existing data.

Neither density-independent (i.e., preferred thermal habitat) nor density-dependent (i.e., cumulative stocking density) factors adequately explain all the observed variation in growth. Results indicate that the density of fall fingerlings plays a major role in determining the density of the forage base. The relation between the preferred thermal habitat and brook trout growth is less clear. At low stocking densities, brook trout growth in unstratified lakes was comparable to that of older brook trout in stratified lakes. This is evidenced by the lack of a significant difference between ages 1+ through 4+ fish in the AFRP lakes, which have a range of stocking densities. Higher stocking densities result in reduced growth, which would probably be most severe for older fish in unstratified lakes. Thus, the interactions between the predator–prey populations and the preferred thermal habitat act simultaneously to regulate brook trout growth. This basic interaction between the two factors becomes complex when other factors, such as spatial distribution and availability of prey, seasonal variability of the preferred thermal habitat, and seasonal distribution and utilization of the thermal habitat by different age fish, cannot be accounted for. Future field studies should incorporate these factors.

Growth is not the only issue affected by warm-water conditions. Brook trout under thermal stress or lack of adequate forage will begin to starve. Starvation leads to reduced activity and other survival strategies (Beamish 1964; Javiad and Anderson 1967), which may eventually lead to mortality as fish attempt to conserve energy. Fish in a weakened condition due to lack of food or thermal stress would probably be more vulnerable to predators, with increased likelihood of mortality from hyperactivity (Black 1958) due to pursuit by predators, or postspawning mortality because of going into the spawning season in poor condition.

Presently, most Adirondack brook trout waters are managed as monoculture systems. In an ideal growth environment, a range of prey sizes should be available for brook trout to achieve maximum potential size at age. A dietary transition from plankton to insects to small fish would occur in systems where forage fish were present. In a brook trout monoculture, maintained by stocking, small

and large trout are in competition for the same invertebrate food source. Since smaller trout are metabolically more efficient and can occupy larger areas of the lake during crucial summer periods, they may outcompete larger fish in a monoculture system. Forage fish introductions may be necessary in thermally marginal waters where large size of brook trout at harvest is the desired management goal.

Conclusions

1. An empirical probability model of lake stratification as a function of maximum depth and water color, developed from the ALSC data base, suggested that shallow (5–10 m maximum depth), low-color (<10 Pt Cobalt units) lakes were the most sensitive to changes in thermal stratification status induced by changes in water color or light attenuation. The model's prediction was verified by observations of changes in color, transparency, and thermal stratification in limed lakes after neutralization and reacidification, where significant changes in transparency and thermal stratification status were observed only in low-color lakes.

2. Shallow (5–10 m maximum depth), potentially sensitive ALSC lakes ($N = 424$) were classified as predominantly weakly stratified (73%), 21% as strongly stratified, and 6% as unstratified. On the basis of an observed 53% decrease in water color in one Adirondack drainage system during 1944–75, we estimated that if a comparable change in color had occurred in all shallow lakes there would have been 22% more strongly stratified lakes present in the 1940's (56% weakly stratified, 43% strongly stratified, and 1% unstratified).

3. Preferred thermal habitat for brook trout was defined as the lake region in the temperature range of 10–16° C, with dissolved oxygen levels greater than 5 ppm. Experimental liming studies demonstrated that the availability and volumetric extent of this habitat is significantly increased as a result of decreased transparency and increased thermal stability after liming of shallow, low-color lakes. Reacidification of these lakes resulted in decreases in the availability of preferred brook trout habitat.

4. Comparisons of brook trout growth in unstratified and stratified Adirondack lakes revealed significantly greater mean weights for older (> age 2), larger brook trout in stratified lakes, but no significant effects of stratification on growth of young (age 1) trout. The smaller fish did not seem to be constrained by the observed midsummer thermal conditions in Adirondack lakes, but growth seemed to be strongly density dependent.

5. Simulations of brook trout growth in unstratified and stratified lakes also predicted an increasing differential in weight at age between the lake types as a result of summer reductions in growth rate of brook trout in warm, unstratified lakes. This analysis also indicated that sustained growth in unproductive Adirondack waters of older brook trout (greater than age 2), beyond an approximate threshold of 500–600 g body weight, requires the availability of low (<16° C) summer water temperatures that would only be available in stratified lakes.

6. High population density and limitations in the availability or extent of preferred thermal habitat in shallow Adirondack lakes are of primary significance in determining population growth patterns and limiting maximum size at age for older age classes of brook trout.

7. Brook trout populations presently most susceptible to negative impacts from acidification-induced increases in transparency and consequent reductions in preferred thermal habitat occur primarily in shallow, low-color lakes that are marginally acidified and either weakly stratified or strongly stratified with anoxic hypolimnia. On the basis of results of experimental liming studies (LAMP and ELS), significant improvements in brook trout thermal habitat can be achieved in these lakes by reducing acidity levels.

Acknowledgments

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Appendix

Appendix Table 1. *Observed growth in brook trout (*Salvelinus fontinalis*) in strongly stratified Adirondack Fishery Research Program lakes, 1979–90.*

Lake	Age (years)	Sample (*n*)	Mean length (millimeters)	Mean weight (grams)
Chambers	1	293	245.9	142.8
	2	41	292.6	228.8
	3	2	315.0	322.1
Fourth Bisby	1	778	284.3	237.2
	2	238	362.1	510.2
	3	40	408.9	762.0
	4	7	438.3	898.0
Goose	1	534	251.2	171.7
	2	142	309.7	322.7
	3	13	352.2	507.8
	4	2	356.8	476.3
Green	1	12	277.2	195.3
	2	26	348.8	458.2
	3	7	403.1	666.3
	4	1	452.0	1,134.0
Otter	1	330	255.5	173.3
	2	137	310.8	311.4
	3	21	345.2	409.7
	4	3	364.1	603.3

Appendix Table 2. *Observed growth in brook trout (*Salvelinus fontinalis*) in weakly stratified Adirondack Fishery Research Program lakes, 1979–90.*

Lake	Age (years)	Sample (*n*)	Mean length (millimeters)	Mean weight (grams)
Canachagala	1	350	271.1	215.4
	2	395	351.4	481.9
	3	21	418.9	578.1
	4	11	457.2	961.6
Mountain	1	717	271.4	194.5
	2	188	317.9	309.7
	3	57	317.5	317.2
	4	20	328.2	328.2

Appendix Table 3. *Observed growth in brook trout (*Salvelinus fontinalis*) in unstratified Adirondack Fishery Research Program lakes, 1979–90.*

Lake	Age (years)	Sample (*n*)	Mean length (millimeters)	Mean weight (grams)
Deer	1	639	275.4	206.5
	2	148	337.1	385.2
	3	30	382.8	619.3
	4	2	375.9	444.5
Jones	1	14	185.4	54.4
	2	5	251.5	145.2
	3	4	274.3	199.6
	4	1	302.3	263.1
Rock	1	433	267.9	155.8
	2	48	386.6	574.9
	3	5	434.3	912.7
	4	8	403.9	777.4
Wheeler	1	48	243.7	129.9
	2	71	287.4	206.7
	3	76	322.1	280.6
	4	3	381.0	536.7

Appendix Table 4. *Regression analysis for the relation between mean weight, preferred thermal habitat, and stocking density in Adirondack Fishery Research Program lakes for age 1+ brook trout (*Salvelinus fontinalis*).*

Type	Independent variables	Coefficient	P (2-tailed)	Adjusted R^2	ANOVA F-ratio	ANOVA P
Simple regression						
	$X1$	0.000	0.291	0.004	1.148	0.291
	$X2$	0.001	0.823	0.000	0.051	0.823
	$X3$	-0.003	0.000	0.293	17.606	0.000
	$X4$	-0.003	0.000	0.293	17.606	0.000
Multiple regression						
	$X1$	-0.000	0.863	—	—	—
	$X3$	-0.003	0.000	—	—	—
				0.275	8.599	0.001
	$X1$	-0.000	0.863	—	—	—
	$X4$	-0.003	0.000	—	—	—
				0.275	8.599	0.001
	$X2$	-0.001	0.892	—	—	—
	$X3$	-0.003	0.000	—	—	—
				0.275	8.591	0.001
	$X2$	-0.000	0.892	—	—	—
	$X4$	-0.003	0.000	—	—	—
				0.275	8.591	0.001

Appendix Table 5. *Regression analysis for the relation between mean weight, preferred thermal habitat, and stocking density in Adirondack Fishery Research Program lakes for age 2+ brook trout* (Salvelinus fontinalis).

Type	Independent variables	Coefficient	*P*(2-tailed)	Adjusted R^2	ANOVA *F*-ratio	ANOVA *P*
Simple regression						
	*X*1	0.000	0.029	0.101	5.162	0.029
	*X*2	0.002	0.795	0.000	0.068	0.795
	*X*3	-0.005	0.000	0.459	32.329	0.000
	*X*4	-0.003	0.000	0.536	43.759	0.000
Multiple regression						
	*X*1	0.000	0.321	—	—	—
	*X*3	-0.005	0.000	—	—	—
				0.459	16.677	0.000
	*X*1	0.000	0.405	—	—	—
	*X*4	-0.002	0.000	—	—	—
				0.532	22.059	0.000
	*X*2	-0.002	0.697	—	—	—
	*X*3	-0.005	0.000	—	—	—
				0.445	15.862	0.000
	*X*2	-0.002	0.730	—	—	—
	*X*4	-0.003	0.000	—	—	—
				0.524	21.406	0.000

Appendix Table 6. *Regression analysis for the relation between mean weight, preferred thermal habitat, and stocking density in Adirondack Fishery Research Program lakes for age 3+ brook trout* (Salvelinus fontinalis*)*.

Type	Independent variables	Coefficient	P(2-tailed)	Adjusted R^2	ANOVA	
					F-ratio	P
Simple regression						
	$X1$	0.000	0.014	0.186	6.935	0.014
	$X2$	0.007	0.551	0.000	0.365	0.551
	$X3$	-0.008	0.000	0.582	37.202	0.000
	$X4$	-0.002	0.000	0.695	60.159	0.000
Multiple regression						
	$X1$	0.000	0.108	—	—	—
	$X3$	-0.008	0.000	—	—	—
				0.610	21.335	0.000
	$X1$	0.000	0.217	—	—	—
	$X4$	-0.002	0.000	—	—	—
				0.702	31.613	0.000
	$X2$	0.004	0.599	—	—	—
	$X3$	-0.008	0.000	—	—	—
				0.570	18.211	0.000
	$X2$	0.002	0.818	—	—	—
	$X4$	-0.002	0.000	—	—	—
				0.683	28.968	0.000

Appendix Table 7. *Regression analysis for the relationships between mean weight, preferred thermal habitat, and stocking density in Adirondack Fishery Research Program lakes for age 4+ brook trout (*Salvelinus fontinalis*).*

Type	Independent variables	Coefficient	P(2-tailed)	Adjusted R^2	ANOVA F-ratio	ANOVA P
Simple regression						
	X1	0.000	0.049	0.173	4.553	0.049
	X1	0.000	0.049	0.173	4.553	0.049
	X2	0.019	0.312	0.005	1.091	0.312
	X3	-0.006	0.003	0.490	49.385	0.000
	X4	-0.002	0.000	0.740	49.385	0.000
Multiple regression						
	X1	0.000	0.221	—	—	—
	X3	-0.005	0.002	—	—	—
				0.431	7.437	0.006
	X1	0.000	0.374	—	—	—
	X4	-0.002	0.000	—	—	—
				0.737	24.868	0.000
	X2	0.012	0.423	—	—	—
	X3	-0.006	0.004	—	—	—
				0.396	6.583	0.009
	X2	0.008	0.452	—	—	—
	X4	-0.002	0.000	—	—	—
				0.733	24.366	0.000

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